UNIVERSITY OF CALIFORNIA

Santa Barbara

The Influence of the Human Stress Response on Navigation Strategy and Efficiency

A dissertation submitted in partial satisfaction of the requirements for the degree Doctor of Philosophy in Psychological and Brain Sciences

by

Alexander Paul Boone

Committee in charge: Professor Mary Hegarty, Chair Professor Barry Giesbrecht Professor Emily Jacobs Professor Daniel Montello

June 2019

The dissertation of Alexander Paul Boone is approved.

 \mathcal{L}_max , and the set of the

 \mathcal{L}_max and the contract of the contrac

 \mathcal{L}_max , and the set of the

 \mathcal{L}_max and the contract of the contrac

Barry Giesbrecht

Emily Jacobs

Daniel Montello

Mary Hegarty, Committee Chair

June 2019

The Influence of the Human Stress Response on Navigation Strategy and Efficiency

Copyright © 2019

by

Alexander Paul Boone

ACKNOWLEDGEMENTS

The process of conducting science is a lot like being in the woods. You may know how you got there and finding the way out is not always easy, but sometimes being lost is half the fun. In science, like life, there are no shortcuts. The more you figure out, the more you realize that many more questions lie before you. Understanding this has been a long outbound journey. Here, I point back to the start to thank everyone that has helped me along the way.

My family, in its entirety, has in some way or another shaped core aspects of my interests in the world. Of course, it is hard to succinctly express all of the ways. Therefore, I just want to say thank you for each nugget of wisdom, whether intentional or accidental.

I have to express my deepest gratitude to my mentor, Mary Hegarty, who promoted me at every possible opportunity in graduate school. I truly appreciate the sustained patience without which I would still be walking circles in the woods. I have greatly appreciated our time working together.

I also have to thank my committee which provided the critical knowledge and comments that shaped this work. I appreciate the opportunity afforded me by Barry Giesbrecht in bringing me onto the Boss team to carry out some of the work presented here.

I am deeply indebted to the entire Boss team (Michael Miller, Scott Grafton, Mary MacLean, Tom Bullock, Tyler Santander, Gold Okafor, Jamie Raymer, Rory Flemming, Liann Jimmons, Alex Stuber) for their assistance in science and life. I would also like to thank all of the undergraduates that have helped me during graduate school, in particular: Jared Gong, Bryan Maghen, David Sañosa, Lindsey Nguyen and Arhan Shetty. I also need to shout out to the Trier team (Shaina Michalowicz, Doyna Heyddati, Soniya Palwankar, Kelsey Almassey, Yasna Mehrabani, Miranda Lee, Marie Jung, Rebecca Bronstein, Monica Phoung, Shweta Pahade, Lizi Xian, Katie Peterson, Daliana Reyes, Albany Turcio, Tal Sahar, Jasmine Feng, Abigail Ragasa, Maya Sydir) because they did excellent work stressing people out.

I want to thank the entire UCSB spatial community and the Hegarty Lab in particular (Peri Gunalp, Carol He, Heather Burte, Trevor Barrett, and Margaret Tarampi). Further, I would like to thank everyone involved in the cognition seminars, especially Rich Mayer. The conversations and thoughts we have shared over the years were vital towards this dissertation in many ways.

I want to thank all the participants: the ones that got sick, the ones that didn't, the ones I stressed, and the ones that had fun.

I have to thank my wife, Chelsea, for putting up with this and always encouraging me in every way. Eliza, thank you for reminding me daily that the world is full of wonder.

VITA OF Alexander Paul Boone June 2019

Education

Bachelor of Arts, History Bachelor of Arts, Psychology Undergraduate Honors Thesis: "Exploring the limits of the focus of attention"

Research Interests

In a broad sense, I am interested in how individuals strategize in spatial thinking as these strategies inform various domains and educational contexts. The strategies we use for tasks such as mental rotation and interpreting uncertainty in visualization of data play a crucial role in STEM domains. Further, I am interested in exploring how our strategies are shaped by experience and methods that tease those strategies from performance such as where we look for particular patterns in data. More recently, my research has focused on human navigation strategies and how they may be separable from our navigation ability and how our navigation strategies and abilities are influenced by hormonal changes that arise from the human stress response.

Publications

- **Boone, A. P.**, Maghen, B. & Hegarty, M. (2019). Instructions Matter: Individual and Sex Differences in Navigation Strategy and Ability. *Memory & Cognition*. doi.org/10.3758/s13421-019-00941-5
- **Boone, A. P.**, Gong, X., & Hegarty, M. (2018). Sex differences in navigation strategy and efficiency. *Memory & Cognition*, *46*(6), 909-922. doi.org/10.3758/s13421-018- 0811-y
- **Boone, A. P.**, Gunalp, P., & Hegarty, M. (*2018*). Explicit versus actionable knowledge: The influence of explaining graphical conventions on comprehension of hurricane forecast visualizations. *Journal of Experimental Psychology: Applied*, *24*(3), 275 -295. DOI:10.1037/xap0000166
- Bellatore, A., Gordon, D., & **Boone, A. P.** (2018). The sonification of data uncertainty. *Cartography and Geographic Information Science.* DOI: 10.1080/15230406.2018.1495103
- Hegarty, M., Burte, H., & **Boone, A. P.** (2018). Individual differences in spatial abilities and strategies. In D. R. Montello (Ed). Handbook of Behavioral and Cognitive Geography (pgs 231-246). Cheltenham: Edwin Elgar Publishing.
- **Boone, A. P.**, & Hegarty, M. (2017). Sex differences in mental rotation tasks: Not just in the mental rotation process! *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *43*(7), 1005-1019. http://dx.doi.org/10.1037/xlm0000370
- Liu, L., **Boone, A. P.**, Ruginski, I., Padilla, L., Hegarty, M., Creem-Regehr, S., Thompson, W., Yuksel, C., & House, D. H. (2017). Uncertainty visualization by representative sampling from prediction ensembles. *IEEE Transactions on Visualization and Computer Graphics, 23*(9), 2165-2178. doi: 10.1109/TVCG.2016.2607204
- Hegarty, M., Friedman, A., **Boone, A. P**., & Barrett, T. J. (2016). Where are you? The effect of uncertainty and its visual representation on location judgments in GPS-like displays. *Journal of Experimental Psychology: Applied*, *22*(4), 381-392. http://dx.doi.org/10.1037/xap0000103
- Kastens, K. A., Shipley, T. F., **Boone, A. P.**, & Straccia, F. (2016). What geoscience experts and novices look at, and what they see, when viewing data visualizations. *Journal of Astronomy and Geoscience Education*, 3(1), 27-58. doi: 10.19030/jaese.v3i1.9689.
- Ruginski, I. T., **Boone, A. P.**, Padilla, L. M., Liu, L., Heydari, N., Kramer, H., Hegarty, M., Thompson, W. B., House, D. H., Creem-Regehr, S. H. (2016). Non-expert interpretations of hurricane forecast uncertainty visualizations. *Spatial Cognition & Computation*, 16(2), 154-172*. doi:* 10.1080/13875868.2015.1137577
- Blume, C. L., **Boone, A. P.**, & Cowan, N. (2015). On the use of response chunking as a tool to investigate strategies. *Frontiers in Psychology*, *6*, 1942.
- Ormand, C. J., Manduca, C., Shipley, T. F., Tikoff, B., Harwood, C., Atit, K., and **Boone, A. P.** (2014). Evaluating geosciences students' spatial thinking skills in a multiinstitutional classroom study. *Journal of Geoscience Education, 62*(1), 146-154.

Manuscripts Under Review

Friedman, A., Kohler, B., Gunalp, P., **Boone, A. P.**, & Hegarty, M. (*Under Review*). A computerized spatial orientation test. Resubmitted to *Behavior Research Method*.

Academic Presentations and Posters

MacLean, M. H., **Boone, A. P.**, Bullock, T., Santander, T., Raymer, J., Stuber, A., Jimmons, L., Okafor, G. N., Grafton, S. T., Miller, M. B., & Giesbrecht, B. (2019, May). Acute Stress Alters the Priorty of salient feared, but not neutral, distracters. Poster presented at Vision Science Society, St. Pete Beach, FL, USA.

- Bullock, T., MacLean, M. H., **Boone, A. P.**, Santander, T., Raymer, J., Jimmons, L., Stuber, A., Okafor, G. N., Grafton, S. T., Miller, M. B., & Giesbrecht, B. (2019, May). Physical, mental and social stress selective modulate inhibitory control during search of natural scenes. Poster presented at Vision Science Society, St. Pete Beach, FL, USA.
- Santander, T., MacLean, M. H., Bullock, T., **Boone, A. P.**, Raymer, J., Jimmons, L., Stuber, A., Okafor, G. N., Grafton, S. T., Giesbrecht, B., & Miller, M. B. (2019, March). Identifying biomarkers to predict behavioral responses to stress in criterion shifting during recognition memory. Poster presented at Cognitive Neuroscience Society, San Francisco, CA, USA.
- **Boone, A. P.**, Maghen, B. & Hegarty, M. (*2018, June*). Do Task Instructions Matter? Individual Differences in Navigation Strategy in Virtual Environments. Talk presented at Interdisciplinary Navigation Symposium 2018, Mont Tremblant, Quebec, Canada.
- Hegarty, M., **Boone, A. P.,** & Gunalp, P. (2017, November). Effects of verbal instructions on non-expert interpretations of hurricane forecast uncertainty visualizations. Poster presented at Psychonomics Society, Vancouver, British Columbia, Canada.
- **Boone, A. P.**, Gong, X., Sañosa, D. & Hegarty, M. (2016, August). Individual differences in navigation efficiency and strategy using the dual solution paradigm. Talk presented at Spatial Cognition Conference, Philadelphia, PA.
- **Boone, A. P.**, Gunalp, P., Heydari, N., & Hegarty, M. (2016, August). Effects of verbal instructions on non-expert interpretations of hurricane forecast uncertainty visualizations. Poster presented at Spatial Cognition Conference, Philadelphia, PA.
- Friedman, A., Hegarty, M., **Boone, A. P.**, & Barrett, T. J. (2016, August). Where are you? The effect of uncertainty $\&$ its visual representation on location judgments in GPSlike displays. Poster presented at Spatial Cognition Conference, Philadelphia, PA.
- Hegarty, M., Burte, H., **Boone, A. P.**, Heydari, N & Tarampi, M. (2015, September). Individual differences in spatial abilities across different scales of space. Presented at the 6th International Conference on Spatial Cognition, Rome, Italy.
- **Boone, A. P.** & Hegarty, M. (July 2015). Strategy differences do not account for gender difference in mental rotation. Poster presented at Cognitive Science Society, Pasadena, CA.
- Ruginski, I. T., **Boone, A. P.**, Padilla, L., Hegarty, M., Thompson, W. B., & Creem-Regehr, S. H. (July 2015). Understanding the Cone of Uncertainty: Non-expert interpretations of hurricane forecast uncertainty visualizations. Poster presented at Cognitive Sciences Society, Pasadena, CA.
- **Boone, A. P.** and Hegarty, M. (September 2014). Twelve years later: The Santa Barbara Sense of Direction scale. Poster presented at Spatial Cognition, Bremen, Germany.
- Kastens, K. A., Shipley, T. F., and **Boone, A. P.** (December 2012). What do geosciences experts and novices look at and what do they see when viewing and interpreting data visualizations? Poster presented at American Geophysical Union, San Francisco, CA.
- Gagnier, K., **Boone, A. P.**, and Shipley, T. F. (November 2012). Looking behavior and penetrative thinking: Examining the relationship between eye movements and performance. Electronic Poster presented at the Geologic Society of America, Charlotte, NC.
- **Boone, A. P.** and Cowan, N. (April 2010). *Exploring the capacity limit of the focus of attention*. Poster presented at the Midwestern Psychological Association, Chicago, IL.

Popular Press Articles

US News and World Report

https://www.usnews.com/news/national-news/articles/2018-05-25/study-menare-better-navigators-than-women

Awards and Honors

President's Dissertation Year Fellowship (2018-2019) Funding of \$24,000 to carry out dissertation research

University of California, Santa Barbara Academic Senate Travel Grant Funding of \$900 to attend iNav in Mont Tremblant, Canada.

Spatial Intelligence and Learning Center Travel Award (September, 2014) Funding of \$1573 to attend 2014 Spatial Cognition Conference in Bremen, Germany.

Raymond Nickerson Best Paper Award 2016 from the Journal of Experimental Psychology: Applied for "Where are you? The effect of uncertainty and its visual representation on location judgments in GPS-like displays."

Best Paper award from the Journal of Geoscience Education for "Evaluating geosciences students' spatial thinking skills in a multi-institutional classroom study."

Academic Research Experience

2013-2019 Navigation Strategies in Virtual Environments Graduate Student Researcher with Dr. Mary Hegarty

Academic Reviews

Ad Hoc Reviewer Memory and Cognition Journal of Cognitive Psychology Behavioural Brain Research Applied Cognitive Psychology Personality and Individual Differences Evolutionary Psychological Science

Conference Paper Reviewer Cognitive Science Society Conference

Undergraduate Mentoring

Professional Memberships

Department Service and Experience

Teaching Assistant Experience

ABSTRACT

The Influence of the Human Stress Response on Navigation Strategy and Efficiency

by

Alexander Paul Boone

Navigating between locations in a known environment is a task we undertake in our daily lives, but not everyone uses the same strategy to navigate. Some people navigate by a route-based strategy of following well-known routes supported by the caudate nucleus while others readily take shortcuts using a hippocampal-dependent place-based strategy (Marchette, Bakker, & Shelton, 2011). Stress is also an everyday occurrence, for most. Interestingly, the largest concentration of the stress hormone cortisol in the brain after a stressor is the hippocampus. Thus, cortisol may influence these navigation strategies differentially such that stress may force place-based navigators into using route-based strategies while route-based navigators may be spared. Further, navigation efficiency may be hindered in either type of navigator. However, little research has been attempted in this area.

To test this prediction in this dissertation, the Dual Solution Paradigm (DSP; Marchette et al., 2011) is used as the navigation task. In this task, participants learn a route in a virtual maze. After learning, participants are placed along the learned route and are asked to navigate between previously learned locations. Each trial is structured such that taking either the learned route or reversing the route lead to the goal; however, in all cases, taking a shortcut is more efficient. After testing, each trial is categorized by strategy selection (e.g., shortcut, learned route) and a measure is computed to assess relative dependence on each type of strategy.

In order to test participants twice, once under stress and once under control conditions, two equivalent mazes were required. The first two experiments in this dissertation were conducted as pilot experiments in order to develop two equivalent mazes for later use. Experiment 1 tested the original DSP maze relative to its mirrored structure and was used to determine the most diagnostic trials. Experiment 1b included more subjects but also reduced the number of trials based on considerations of time. Performance in these mazes was similar, however, the results in Experiment 1b are noticeably weaker than Experiment 1a. These mazes were used for Experiments 2, 3, and 4. For the stress component, three stressors were used: a physiological stressor (Experiment 2), a social stressor (Experiment 3), and a cognitive fatigue stressor (Experiment 4), each presented after the learning phase but before the testing phase.

Experiment 2 used the Cold Pressor Task in which participants place their feet in ice water (stress) and room temperature water (control). Despite differences in cortisol between the two conditions and the subjective measures of stress, there were no differences found between control and stress conditions within individuals in terms of objective strategy measures or efficiency of navigation. Post-hoc analyses of high and low stress responders indicated no differences in navigation between these navigators.

Experiment 3 used the social-evaluative stressor known as the Trier Social Stressor task in which participants prepare and deliver a speech to peers followed by a mental subtraction task (stress) and a speech about their daily routine and a simple addition task (control). In this experiment, differences were found between conditions for subjective stress and in cortisol between the control and the stress condition. However, no differences were found between control and stress conditions within individuals in navigation strategy or

xii

efficiency of navigation. Post-hoc analyses of high and low stress responders indicated no differences in navigation between these navigators.

Experiment 4 used a mental fatigue task in which participants schedule workers on various tasks with increasing difficulty per trial (stress) and a simple word search task (control) for a two-hour period. Here, differences were found between conditions for subjective stress relating to the stressor, but no differences were found in cortisol between the control and the stress condition. Further, no differences were found between control and stress conditions within individuals in navigation strategy or efficiency. Post-hoc analyses of high and low stress responders indicated less shortcuts and less efficient navigation in those responding *less* to the scheduling task stressor. This results suggests a possible facilitation of navigation behavior when under acute stress.

This work indicates several important conclusions. First, navigation strategy and efficiency may be robust to the effects of various stressors may have little influence over our navigation strategy systems in virtual environments. Navigation strategy remains stable even in the presence of stressful stimuli. Differences found between the Experiment 1b and the stressor studies indicates a potential stress effect in the controlled lab setting, such that participants took generally fewer shortcuts in Experiment 1b compared to both the Experiment 2 (cold pressor) and Experiment 4 (cognitive fatigue). Results are discussed in the context of the overarching cognitive theory as well as it's connection to other task domains such as emergency egress.

xiii

TABLE OF CONTENTS

I. Introduction

Imagine that you are working in your office when you get a phone call that a family member has been in an accident at their work. You must now leave work to be with them. At this point, you will need to exit your office, walk to your vehicle, and then navigate to their location in an efficient manner, doing so while under stress. Thankfully we do not have this experience often, but stress and navigation are two aspects of life that we face daily. Interestingly, the human stress response and our navigation systems may interact in important ways given that both systems are associated with the hippocampus; however, there is paucity of research exploring this interaction. The research that does exist in this topic indicates mixed results. A better understanding of how these two systems work together has implications for a diverse set of applications such as emergency egress (Ozel, 2001), military operations, and even traffic flow algorithms in densely populated areas.

The focus of this dissertation is on the influences of stress on navigation strategy, as a special case of memory, in a navigation task. The goal is to understand if psychological, physiological, and cognitive stressors, through the release of cortisol, could alter how typically good navigators choose to carry out navigational tasks. More specifically, the question is: if cortisol blocks a good navigator's ability to take shortcuts by overloading hippocampal pyramidal place cells with glucocorticoid binding, then these navigators may be forced to rely on well-learned routes. That is, I predict that when under conditions of stress, good navigators will rely on well-learned routes while poor navigators will remain unaffected. Next, I predict that these effects will be mediated by cortisol.

Chapter II of this dissertation will present research findings concerning two navigation strategies and the brain areas associated with each, followed by specific details of the Dual Solution Paradigm (DSP; Marchette, Bakker, & Shelton, 2011), a task that has been used to investigate navigation strategies objectively. Chapter II will also focus on a physiological description of the human stress response. Various techniques of stress induction in controlled laboratory settings will be described along with research findings concerning stress and human memory generally. Next, research that has specifically explored the interaction between the navigation and stress systems will be elucidated.

Chapter III presents the findings of two pilot experiments conducted utilizing a previously validated Dual Solution Paradigm (DSP) in order to evaluate the equivalence of two environments to be used in this dissertation. Experiment 1a presents a within-subjects experiment assessing the equivalence of two environments that are structurally the same but mirrored. Here, strategy and performance were similar across mazes. Experiment 1b uses the same design and environment but includes more participants to balance the gender of participants. In this experiment, the number of trials was reduced. Results indicated a similar pattern to Experiment 1a and thus these two environments and trials were used in later experiments.

Chapter IV presents three studies conducted to investigate the effect of stress on navigation strategy and efficiency. These studies used a within-subject design across two sessions (stress vs control). Experiment 2 utilized a physiological stressor known as the Cold Pressor task in which participants place their feet in an ice water bath for a period of 90s (stress) or a room-temperature water bath (control). Experiment 3 used a psychosocial stressor known as the Trier Social Stressor task in which participant prepare and deliver a

speech in front of peers before completing a vocal subtraction task (stress) and prepare and deliver a speech absent peers before completing a vocal addition task (control). Experiment 4 used a cognitive fatigue stressor in which participants perform a scheduling task of increasing difficulty and mental effort (stress) or a word search (control) for 120 minutes. The results of these experiments are discussed.

In Chapter V, an analysis across each of the three stressor conditions to compare and contrast behavior between them is presented. Interestingly, this data suggests that stress may shape our strategy and efficiency of navigation more subtly than expected. For instance, in two stressors, the distributions of strategy and efficiency in the stress condition are more centralized around the mean whereas in the control conditions, the distributions are more uniform. Further, I compare the behavior in each stressor experiment to the data from Experiment 1b in order to examine differences. While the physiological and cognitive fatigue experiments (Experiments 2 and 4, respectively) showed more shortcuts and better efficiency in both the stress and control conditions, no differences were found between Experiment 1b and Experiment 3. Several possibilities for this pattern are explored.

Finally, in Chapter VI, the combined results and their implications for the theory of stress and navigation are discussed. Given that stress did not alter navigation strategy and efficiency in the way predicted, several alternative explanations of this effect are explored followed by final thoughts and conclusions of this work.

II. Background

Navigation Strategy and the Brain

Navigation is a cognitively complex, and goal-oriented, task which involves the combination of locomotion (e.g., running, walking) and wayfinding (e.g., planning, problem solving; Montello, 2005). While we know there are individual differences in large-scale spatial cognition such as ability to learn an environmental layout (Ishikawa & Montello, 2006) as well as in self-reported environmental spatial ability (Hegarty, Richardson, Montello, Lovelace, $\&$ Subbiah, 2002), there are also individual differences in navigation strategy (Lawton, 1994; Lawton & Kallai, 2002; Lawton, Zieles, & Charleston, 1996; Marchette, Bakker, & Shelton, 2011; Furman, Clement-Stevens, Marchette, & Shelton, 2014).

A tale of two strategies. Here, I will focus on two navigationally distinct strategies: the *place* strategy and the *response* strategy of navigation. Each navigation strategy largely comes down to what information someone encodes, remembers, and recalls about the environment in which they wish to navigate. A wealth of evidence from animal and human neuroscience suggests that there are two primary navigation strategies governed by different brain structures, a place-based strategy and a response-based strategy (O'Keefe & Nadel, 1978; Packard & McGaugh, 1996; Maguire, Burgess, Donnett, Frackowiak, Frith, & O'Keefe, 1998; Iaria, Petrides, Dagher, Pike, & Bohbot, 2003; Marchette et al., 2011; Furman et al., 2014).

Consider the following example of how each strategy plays out in work using the rodent, presented in Figure 1. Imagine the typical rodent plus-maze with four equal length walkways intersecting in the middle placed in a typical lab setting with various items affixed

to the walls serving as navigational cues. On each day of training, a rat is placed in the maze and allowed to explore until it finds a treat (cheese) at the end of an adjacent walkway. Over the course of training, the rat learns to walk down the initial walkway and make a right to obtain the treat. After training to criterion, the rat is placed in the opposite side of the plus maze (i.e., 180 degree environmental rotation) and is required to find the treat. Importantly, the scent of the treat has been obscured to ensure that the rat cannot use any smell cues to navigate but is rather has to rely on other cues, external (e.g., landmarks) and/or internal (e.g., cell firings). The turn that the rat makes at the confluence of the walkways depends on what information the rat is using to navigate. If the rat operates purely on the responses it made while initially learning, it will turn right incorrectly and fail to get the cheese. However, if the rat noticed the cues on the walls while learning and subsequently uses those cues to navigate, the rat will be able to make the appropriate adjustment and turn left to obtain the reward.

Figure 1. Schematic representation of how each navigation strategy plays out in a T-maze task. The mouse learns the rewards is in the right arm of the T-maze. At test (right panel), the mouse choses the direction. Rightward choice indicates route response navigation, while leftward choice reflects coordination with the environment feature for place based navigation. This schematic is adapted from Marchette et al. (2011).

Given this example, the *place strategy* of navigation depends on having environmental (whether graph or survey) knowledge of the environment and is characterized by flexible spatial reasoning enabling navigators to point to unseen locations accurately as well as take shortcuts to goal locations (Kozlowski and Bryant, 1977). This strategy is associated with and is largely dependent upon the hippocampus (Morris, Garrud, Rawlins, & O'Keefe, 1982; Sutherland, Kolb, & Whishaw, 1982), which brings spatial relations together in order to form an integrated mental representation of the environment. This process involves a variety of special spatial neurons including place cells (O'Keefe & Nadel, 1978; O'Keefe & Dostrovsky, 1971). Place cells are pyramidal cells located within the cornu ammonis subfields (CA1 and CA3) of the hippocampus proper and also in the subiculum and the entorhinal cortex of the overall hippocampal formation (O'Keefe, 2007). These cells take in both in-flowing perceptual information including idiothetic proprioceptive information such as from the knee and ankle joints (Bird & Burgess, 2008) in order to fire when the organism passes through a specific region within the environment (known as a place field). It is thought that these place cells and place fields, along with other spatially relevant neurons, give rise to what has been termed the "cognitive map" by various researchers throughout the literature (O'Keefe and Nadel, 1978) supporting place strategy navigation.

On the other hand, the *response strategy* of navigation is characterized by reliance upon the sequence of stimulus response actions made at choice points in the environment during learning. Thus, this strategy is less spatially flexible and does not allow for access of shortcuts in the environment. Using this strategy has been shown to activate the caudate nucleus (CN; Iaria et al., 2003) in fMRI studies. In contrast to the hippocampus, the CN does

not allow for flexible navigational guidance.

Neuroscience evidence in humans has generally supported these distinctions in many studies finding that the hippocampus is activated in expert navigators such as taxi drivers (Maguire et al., 1998; Maguire Woollett, & Spiers, 2006; Kumaran and Maguire, 2005; Schinazi, Nardi, Newcombe, Shipley, & Epstein, 2013) and the CN is more active for those navigating by response-based or non-spatial strategies (Iaria et al., 2003; Bohbot, Lerch, Thorndycraft, Iaria, & Zijdenbos, 2007). Importantly, there is evidence concerning a dissociation of navigation strategies and brain areas in studies in which certain brain areas are rendered temporally inactive. In rodents, the inactivation of the hippocampus leads to more response-like navigation, while the inactivation of the caudate nucleus leads to more placelike navigation (Packard & McGaugh, 1996). This finding indicates that in the absence of one system, the second system may kick in to help the animal achieve navigation goals.

In humans, navigation strategy can be studied both subjectively, through self-report questionnaires, and objectively through observation during a navigation task. Self-report questionnaires have been used most often to assess navigation strategy and preference (Lawton, 1994; Pazzaglia, Cornoldi, & DeBeni, 2000) and indicate that some people prefer use of shortcuts, while others prefer the use of well-learned routes. However, self-report questionnaires rely on a participant's self-knowledge to report their typical strategy, and participants may not always be aware of the strategies they are using. Objective assessment of strategy requires the observation of which strategy is used when someone is given a choice of how to physically navigate an environment. For instance, Lawton, Charleston, and Zieles (1996) used this approach inside of a building. In their experiment, participants were led on a path through a large building and were asked to return to start. Participant walking paths

were coded as shortcuts, partial retrace of the learned path, complete retrace, and as random walking. Unsurprisingly, the shortcut-taking participants took the least time to find the starting location, however, the exact retrace group showed less error in pointing to the starting location. One problem with this study is that participants were only given a single learning trial in which to encode the route.

Given that real-world navigation studies are difficult to perform, researchers have found promise in studying navigation strategy in virtual environments, which allows for more experimental control despite some drawbacks. Building on work in the rodent literature, Marchette, Bakker, and Shelton (2011) conducted a study to investigate route selection after sufficient learning in a virtual environment. These researchers showed participants a video of a path through an enclosed desktop virtual environment along which objects were placed. During retrieval trials, participants were placed on the learned route and asked to navigate between objects in the environment. Participants could navigate by taking either the learned route or by taking a novel shortcut. Trials were categorized as either shortcuts or learned routes by a winner-takes-all strategy of number of steps on each route. Marchette et al. (2011) found a wide range of strategy behavior such that some people take all learned routes while others take all shortcut routes. Further, it was found that the extent to which participants took shortcuts was significantly correlated with their spatial flexibility, as measured by a psychometric perspective taking task (Hegarty & Waller, 2004). Critically, fMRI analysis of route selection in the DSP indicated that participants who took shortcuts showed greater activation in the hippocampus when they learned the maze, whereas response navigators showed greater activations in the caudate nucleus during encoding. These results corroborate previous research indicating a dissociation of strategy and brain activation.

More recently, Boone, Gong, and Hegarty (2018) found similar patterns regarding the individual differences in strategy. However, more route strategies were uncovered. In addition to taking shortcuts and learned routes, participants were found to deviate slightly from the shortcut or the learned route as well as reverse their learned route and wander. Further, this work also extended the individual differences in navigation strategy to efficiency.

To conclude, finding a goal location in a known environment is a cognitively complex task involving different brain areas depending on how the navigator initially encodes the environment. Some navigators use the spatially flexible place strategy relying on the hippocampal formation enabling shortcutting behavior. Other navigators use stimulus response actions such as following well-known routes, which has shown activations of the caudate nucleus. It is important to note that these areas are engaged simultaneously and both strategies can lead to successful navigation. While the hippocampal formation is central to memory (Scoville & Milner, 1957) it is also relevant for other processes such as regulation of the human stress response (de Kloet, Oitzl, & Joëls, 1993). In the following section, the human stress response system will be reviewed in the context of its mechanisms, the types of events that elicit this response, as well as the results of research exploring the influence of stress on memory.

Stress

As navigation is a ubiquitous part of our lives, so too is the experience of stress states. Stress can be either adaptive or detrimental pursuant to the dose of the stressor, such as illustrated by the Yerkes-Dodson effect indicating that too little or too much stress can lead to poor performance while moderate stress can lead to enhanced performance (Yerkes &

Dodson, 1908). In particular, stressors play a critical role in memory and cognition. Take, for instance, test performance anxiety in which a student "goes blank" at the start of the exam. This section explores how the stress response system operates, the laboratory tasks that elicit a reliable response from this system, how the stress response is measured, followed by a review of literature concerning the effects of acute stress on memory and navigation.

The Human Stress Response. The human body operates on a 24-hour circadian cycle of stress hormone secretions, such as glucocorticoids, with a large dose released right before we wake up, but declining throughout the day and into the evening. During wake periods, external stressors lead to additional pulses of glucocorticoid secretion into the blood stream (Lupien, Maheu, Tu, Fiocco, & Schramek, 2007). External stressors can activate two different pathways within our bodies, the sympathetic nervous system and the Hypothalamic-Pituitary-Adrenal (HPA) axis, which both serve to divert energy to parts of the body necessary for dealing with the stressor, such as, the brain and muscles. In terms of the HPA axis, when a human comes into contact with a physical or psychological stressor it sets off a chain of physiological events within the body starting with the hypothalamus releasing corticotropin-releasing hormone, which in turn causes the pituitary gland to release adrenocorticotropic hormone, and finally the adrenal gland releases glucocorticoids such as cortisol (Sapolsky, 2002; Kemeny, 2003; Lupien et al, 2007). The stress hormones including glucocorticoids like cortisol, and catecholamines like norepinephrine, travel through the blood stream; however, only the glucocorticoids are able to pass the blood brain barrier (Lupien et al., 2007). Once in the brain, cortisol binds to specific receptors that help the body regulate the stress response (de Kloet et al., 1993). Importantly, the largest concentration of glucocorticoids in the brain after a stressor is the hippocampus (McEwen et al., 1968), a site

necessary for memory (Scoville & Milner, 1957).

Glucocorticoids such as cortisol can bind to two receptor sites in the brain known as mineralocorticoid receptors (MR) and glucocorticoid receptors (GR). Although these receptors bind with glucocorticoids, they have different distributions in the brain, as well as different affinities for glucocorticoids that change throughout the day (Lupien et al., 2007). MR sites are found in limbic structures, such as the amygdala, while GR sites are distributed in the frontal area (Lupien et al., 2007), but importantly these receptors are collocated in the hippocampus (Herman, Patel, Akil, & Watson, 1989). In the morning and during/after a stressful period, both receptor types are activated; while in the evening mainly the MRs remain activated (Lupien et al., 2007).

Acute stress induction in the laboratory. Acute stress can be induced through two methods. First, stress can be induced when participants ingest a cortisone pill, which the body converts to cortisol and the body reacts accordingly. This method reliably increases cortisol and allows for greater control over experimental stress induction conditions. Another method to increase acute stress hormones in humans is through a participant's reaction to external stimuli. These induction techniques can be psychosocial, such as those in which social evaluation takes place, uncontrollable or unpredictable circumstance (Dickerson $\&$ Kemeny, 2004; Gagnon & Wagner, 2016), or physical induction such as subjecting parts of the body to cold temperatures as is done in the Cold Pressor Test (CPT; Hines & Brown, 1932; Larra et al., 2017).

In terms of psychosocial stressors, one task that has shown marked reliability in human corticosteroid release is the Trier Social Stressor Test (TSST; Kirschbaum, Pirke, & Hellhammer, 1993; Birkett, 2011). In this task, naïve participants are brought into a lab

setting and settled to baseline for a period of time before being told that they must produce a speech on a given topic to a group of peer assessors. After the preparation period of ten minutes, the participant is placed in front of the panel of assessors. At this point the participant must give their prepared speech for five minutes. If the participant stops speaking for a period of 20 seconds, a panelist prompts the participant to continue speaking. At the conclusion of five minutes of speaking, the participant is asked to verbally subtract a number (e.g., 13) from a larger number (e.g., 1022) in front of the panel for five minutes. If the participant says an incorrect value, they are asked to start over. This task has shown a cortisol increase of up to four fold from baseline as well as other hallmarks of HPA axis activation such as heart rate increase (Kirschbaum et al., 1993). However, this and other research indicates that humans vary in the amount of cortisol they elicit to stressors and further research has shown sex differences in cortisol reactivity showing that males have a larger cortisol response (Kirschbaum, & Hellhammer, 1989; Kirschbaum et al., 1993).

In terms of physical stressor induction, the Cold Pressor Test (CPT; Hines & Brown, 1932; Lovallo, 1975) has shown marked increases in stress hormone release. In this task, participants are required to submerge their arm in cold water (approximately 0˚ - 4˚ C) up to just above the elbow for up to three minutes, and are allowed to remove their arm at any time (cf. Buchanan, Tranel, & Adolphs, 2006). Despite research indicating large increases in cortisol after cold pressor tasks (Andreano & Cahill, 2003; Smeets, Otgaar, Candel, & Wolf, 2008), other studies have indicated that cortisol release in this task is not consistent (al'Absi, Petersen, & Wittmers, 2002). Finally, cognitive stressors such as the star mirror tracing task have not always shown cortisol increases (Richardson & VanderKaay Tomasulo, 2016)

Given that there are various methods in which acute stress can be induced in the lab

and those methods vary in their effectiveness to increase cortisol, Table 1 presents a comparison of stressor protocols including meta-analytic values of control participants. This table illustrates several important points. First, morning testing sessions reveal larger cortisol response indicating that time of day is an important aspect of experimental design decisions. Second, cortisone pills and biking stressors leads to a very large salivary cortisol response similar to exogenous administration while other tasks indicate lower responses, although larger than controls.

Measuring the stress response. Due to the individual differences in stress response (Kudielka, Hellhammer, & Wüst, 2009; Kirschbaum, Wüst, & Hellhammer, 1992; O'Connor & Corrigan, 1987), the secretion of cortisol must be measured several times during an experiment session. The amount of cortisol that is released due to a specific stressor can be measured through blood, urine, and salivary samples. Cortisol in blood and urine is difficult to relate to a specific stressor as void periods (i.e., urination) are not typically in phase with the onset of the particular stressor of interest. Cortisol found in saliva is "unbound" and is directly relatable to the stressor of interest (Baum & Grunberg, 1997). Therefore, cortisol is most often measured through saliva samples. This method requires participants to salivate into a collection tube, which is then sent to a lab for which several techniques, such as radioimmunoassay, are used to quantify cortisol. Kirschbaum and Hellhammer (1989) present normative values for several time points throughout the day (see Table 1); however, ideally, several measurements would take place during the course of a participant's session in order to compare baseline levels to post-stressor cortisol increase.

| | | | | Cortisol |
|--------------------|------|-----------------------|---------------|-----------------|
| Authors | Year | Stressor | Time of Day | (mmol/l) |
| Kirschbaum & | | | | |
| Hellhammer | 1989 | Control | Afternoon | 4.50 ± 3.5 |
| Kirschbaum & | | | | |
| Hellhammer | 1989 | Control | Morning | 14.32 ± 9.1 |
| 25mg Cortisone | | | | |
| de Quervain et al. | 2000 | pill | Not specified | 46.13 |
| O' Connor & | | | | |
| Corrigan | 1987 | Biking | Not specified | 41.4 |
| Kirschbaum et al. | 1993 | TSST | Mixed | 12.5 |
| Schwabe et al. | 2007 | TSST | Not specified | 5.25 |
| Andreano & Cahill | 2006 | CPT | Not specified | 19 |
| Buchanan et al. | 2006 | CPT | Afternoon | 10.55 ± 2.1 |
| Smeets et al. | 2008 | CPT | Afternoon | 9.19 |
| Richardson & | | | | |
| VanderKaay | | | | |
| Tomasulo | 2011 | Mirror Tracing | Morning | 12.5 |
| | | Bilateral Foot | | |
| Larra et al. | 2015 | CPT | Afternoon | 10 |
| | | Paced Auditory | | |
| van Gervan et al. | 2016 | Serial Addition | Morning | 12.04 |

Table 1. Comparison of cortisol release in various stressor protocols in the literature.

Note. Values in this table are approximations based on graphs where tables were not provided or based on averages across similar conditions. All values were converted to nmol/l. Cold Pressor Task (CPT). Trier Social Stressor Test (TSST).

The Influence of Stress on Declarative Memory

Although the physiological effects of stressors on lower animals have been studied for many years since early work pioneered by Selye (1950), it was only after the finding that glucocorticoids are highly abundant in the hippocampus after stress (McEwen et al., 1968) that research started to focused on the effect of stress on memory. This section will be organized into three parts. First, I will describe research on the effect of stress via cortisol on declarative (verbal) memory in humans. Next, I will explore research that has sought to understand the effect of stress on spatial memory in the rodent model. Finally, I will summarize studies of the effect of stress on spatial memory in humans will be explored.

Stress and human declarative memory. The hallmark finding of the effects of stress on memory is that it is a dose-dependent relationship, that is, the inverted U shape (Yerkes $\&$ Dodson, 1908). This research has shown that memory retrieval is related to the amount of cortisol elicited by a stressor such that more cortisol that is released the more memory is impaired (*r* = -.70; Kirschbaum, Wolf, May, Wippich, & Hellhammer, 1996). However, the amount of detriment to memory under stressor conditions depends on several important factors: the phase of memory (encoding, consolidation, retrieval) in which stress is applied (de Quervain, Roozendaal, Nitsch, McGaugh, & Hock, 2000), the arousal elicited to the stimuli to-be-remembered (Wolf, 2009), and the time of day of the study (Het, Ramlow, & Wolf, 2005, Lupien et al., 2007). Despite this conditionality, it is interesting that the impairment effects of stress are found regardless of whether the stressor is psychosocial (Kirschbaum et al., 1996; Smeets, 2011), physical such as foot shocks to rodents (de Quervain, Roozendaal, & McGaugh, 1998), or administered in the form of corticosterone pills (de Quervain et al., 2000).

Research investigating the detrimental effects of cortisol on memory has shown that stressors seem to disrupt only the retrieval memory processes whereas encoding and consolidation are largely unaffected. While it has been shown that stressors typically impair retrieval processes with a medium to large effect size $(d = -0.49)$; Het et al., 2005), the same impairment is not seen when the stressor is placed before encoding or during consolidation (de Quervain et al., 2000, Smeets et al., 2008; Wolf, 2009; Het et al., 2005). As an instructive example, de Quervain et al. (2000) orally administered 25 mg Cortisone pills to three groups of participants. One group received cortisone one hour prior to learning, another group received cortisone just after learning, while the final group received cortisone one hour before retrieval testing. Free recall was only significantly impaired when cortisone was administered prior to testing compared to placebo. Cortisone administration prior to consolidation nor prior to encoding affected free recall. The reason for this deficit during retrieval seems to arise as function of attenuated hippocampal activity. It has been shown that during retrieval under an exogenous stressor, the hippocampi are significantly less active at test compared to baseline within-subject controls (Oei et al., 2007) and lower hippocampal activity can lead to reduced performance in cue recall tasks (de Quervain et al., 2003).

It is worth noting that in terms of consolidation of memory in humans, research is more mixed on the effect of stressors on memory indicating both impairment and enhancement of memory due to effects of the arousal state of the stimuli (Wolf, 2009). For instance, several studies have indicated that the effect of stress on memory consolidation is particular to the level of arousal associated with the stimuli to-be-remembered such that arousing stimuli, such as car accidents, are remembered more (Wolf, 2009; Smeets et al., 2008), sometimes impaired for moderately arousing stimuli (Buchanan et al., 2006), while no

effect (or marginal effect) on memory for neutral stimuli is found (de Quervain et al., 2000; Lupien et al., 2007; Smeets et al., 2008). This is argued to occur in large part due to amygdalar response to various hormones released in response to the stressor (Wolf, 2009).

Finally, although the time of day effect on memory retrieval using various forms of the cold pressor task has not been found (Schwabe et al., 2008; Smeets, 2011), a metaanalysis of 16 published articles using exogenous administration techniques indicated that largest effects on memory impairment happened in accordance with experiment sessions that took place in the morning (Het et al., 2005), when cortisol is already elevated naturally. Given that the largest concentration of cortisol is found in the morning period for humans (Kirschbaum & Hellhammer, 1989), Lupien et al. (2007) argues that the time of day is a critical mediator of memory because both MRs and GRs are highly activated $\sim 100\%$ MR vs $\sim 60\%$ GR) just as they are during stressful events, whereas in the afternoon periods only about 10% of the GRs are activated while 90% of the MRs are activated.

In sum, there are various effects of stress on human memory depending on which phase of memory (encoding, consolidation, retrieval) the stressor is applied, indicating impairments especially for retrieval of arousing but also sometimes neutral stimuli. Further, testing in the morning elicits the largest detrimental memory effects as cortisol levels are naturally elevated at this time. These effects seem to be related to a reduction in hippocampal activity.

Stress and rat spatial memory. The rodent literature has indicated several important findings with respect to spatial memory and stress. First, the effects of stress on memory are not just limited to memory tests using word-lists or images, but extend to spatial memory (de Quervain et al., 1998; Lupien & McEwen, 1997). Secondly, similar to humans, stressors

administered just prior to retrieval are most effective at impairing memory; however, research indicates that consolidation can also be influenced (Lupien & McEwen, 1997; Roozendaal, 2002) specifically related to work investigating the administration of MR and GR antagonist that disrupt spatial memory differentially (Oitzl $\&$ de Kloet, 1992).

Similar to research with humans, work with rodents has indicated that the temporal placement of the stressor relative to testing is important in the context of spatial memory. de Quervain et al (1998) trained rats on eight trials in the Morris Water Maze. After a 24 hour period, foot shocks were given at various time points (2 minutes, 30 minutes, 4 hours) prior to being placed in the Morris Water Maze Task for the free swim probe trial. In this probe trial, memory for the location of the now absent platform is assessed through swim distance and swim time in the appropriate quadrant of the maze. Relative to the 2 minute and 4 hour foot shock groups, only the rats exposed to foot shocks 30 minutes prior to probe trial testing showed elevated blood cortisol levels. It was also these same rats that were impaired on that task, whereas the other rats were unimpaired. This work demonstrates that stressors must be placed at a temporally optimal time to ensure the effects of the stressor (i.e., cortisol) are present at retention testing. This evidence is especially problematic for online stressors such as time pressure in the human literature (reviewed below).

As reviewed above, there has been little evidence for a general effect of stress on memory during consolidation processes for neutral stimuli. In the rodent literature, there is evidence that administration of glucocorticoids just after learning can lead to enhanced memory performance (Sandi, Loscertales, & Guaza, 1997; Roozendaal, 2002). Sandi, Loscertales, and Guaza (1997) showed that rats given a corticosteroid injection after learning in the Morris Water Maze led to enhanced performance during the probe trial. However,

these results were shown to be conditional on how warm the water was during learning (i.e., conditional experience). Those in warmer water received a benefit of post-learning corticosteroid injections whereas those in cooler water did not. Importantly, one difference between the human and rodent literature is the length of consolidation. Typically in the human literature, consolidation *may* be given one hour, whereas with rodents the typical consolidation period is 24 hours. This difference is potentially important when considering the effects of glucocorticoids on memory.

Finally, it has been shown that stress hormone receptors in the brain are critical for explaining the effects of stress on memory during consolidation and retrieval. A blockade of the MRs and GRs leads to differential effects of memory dependent upon which phase of memory an antagonist is administered. Oitzl and de Kloet (1992) showed that which glucocorticoid receptors are activated at retrieval influenced different aspects of spatial learning and memory. In this study, rats were given interbrain injections of an MR antagonist or a GR antagonist meant to block activation of those receptors selectively. Using the Morris Water Maze task, these antagonists were administered either before learning (encoding), just after learning (consolidation), or before testing (retrieval). No differences in swim time in the correct quadrant (the measure of spatial memory) were found between MR antagonist, GR antagonist, or control rats if given before testing (during encoding). However, injecting the rats with their respective antagonist after learning (during consolidation) produced differential patterns at test. Rats given the MR antagonists indicated inefficient search patterns spreading out their swimming across the quadrants of the maze, while rats given GR antagonist prior to or during consolidation took longer to get to platform, but were swimming in the correct quadrant. If injected before learning, rats given the GR antagonist and controls

were no different however the MR rats showed similar effects as being injected during consolidation. Oitzl and de Kloet (1992) offered the explanation that MR antagonists influence "search-escape" behavior while the GR antagonists led to an inability to consolidate spatial information. Although this work considers antagonists meant to block GR/MR binding with glucocorticoids, the stress-spatial memory impairment hypothesis is necessarily concerned with an overabundance of glucocorticoids. Work in humans using MR *agonists* (meant to *stimulate* MR sites) using a virtual Morris Water Maze task showed that the MR stimulation group spent a larger percentage of time navigating in the correct quadrant indicating improved retrieval spatial memory compared to the placebo group (Piber, Schultebraucks, Mueller, Deuter, Wingenfeld, & Otte, 2016). This work indicates that MR stimulation at retrieval may enhance spatial memory.

In sum, work with rodents indicates that the placement of the stressor relative to retention testing, about 30 minutes, is crucial to ensure that participants are sufficiently stressed during a cognitive task. Further, there are various effects of stress on memory depending upon which glucocorticoid receptors are activated or deactivated.

Spatial tasks and stress with humans. What is interesting about navigation and the human stress response is the large amount of overlap between these systems in terms of which brain areas are recruited and which are most impaired by stress. The research reviewed above presents a clear and testable hypothesis. If the brain uses the hippocampus for cognitive map-based navigation and the caudate nucleus for response-based navigation, and stress impairs memories that depend on the hippocampus, then introducing a stressor that elicits cortisol increase should produce selective deficits in performance in those navigators preferring to use the hippocampally-based place strategy. Navigators using a stimulus-

response like navigation strategy (with caudate nucleus activations) should remain unaffected by the application of stressors given that glucocorticoids are not found as readily in this brain area (Defiore, & Turner, 1983).

Researchers have used a variety of methodologies to investigate this hypothesis in humans. Other work that has investigated the role of elicited stress (Trier Social Stressor Task or Cold Pressor) on spatial tasks has been mixed possibly due to a combination of stress protocol type as well as the placement of stressor relative to each phase of memory. Some of these studies have measured cortisol while others have just examined effects of stressor on navigation performance.

More recently, work focused on understanding the effects of stress on spatial memory has endeavored to put participants under stress before solving a task such as exiting a burning virtual building (Meng & Zhang, 2014), pointing to learned locations (Richardson $\&$ VanderKaay Tomasulo, 2016), or even finding their way in previously or newly experienced environments (Brunyé, Wood, Houck, & Taylor, 2016; Ruginski, Stefanucci, & Creem-Regehr, 2018). The common hypothesis tested is the detrimental effect of stress on spatial memory task performance; however, this research indicates mixed, seemingly contradictory results. Sometimes participants rely on previously experienced routes (Brunyé et al., 2018) while other work indicates that participants switch to strategies that rely on some form of complex spatial knowledge (van Gerven, Ferguson, & Skelton, 2016). A review of these studies, as seen in Table 2, indicates that these effects may be partially attributable to several factors such as the particular stress protocol used and the placement of the stress protocol relatively to retrieval. Still, however, this research has indicated that stressors influence navigation behavior in interesting ways.

In one study, researchers were seeking to evaluate how people evacuate buildings while under stress indicated that adding stressor specific stimuli (smoke smell and simulated fire on screen) to the environment leads to longer escape times compared to control participants (Meng & Zhang, 2014). After a brief reading task, meant to calm participants to baseline stress levels, participants were told that the virtual hotel was on fire and they should exit. One group received simulated fire on screen, noise, and a smoky smell in the testing room, while the control group exited under normal conditions. Although the researchers did not measure cortisol, the stress group showed elevated heart rate compared to the control group, which provides some evidence that participants may have been experiencing more stress. Meng and Zhang (2014) found that the stress group took longer to exit the building and traveled longer distances than the control group. This provides preliminary evidence that stress can influence navigation behavior in emergency egress situations, such as when and where people look for signage. However, this study has limitations. Importantly, participants were not given the opportunity to encode the building layout prior to egress. As such, it is unclear what this study reveals, if anything, about navigating from some mental representation of an environment in a stressful scenario. However, this study points to an interesting influence of stress over attention during emergency egress.

Brunyé, Wood, Houck, and Taylor (2016) showed evidence that participants rely on previously experienced routes in the presence of increasing time pressure. Participants were taught a large virtual city via a series of navigation directives between locations. For example, participants were given a goal such as "travel to the pet shop." No navigation directions were given and the next directive was given upon completion of the goal. A day later participants were required to navigate between previously learned locations under

increasing levels of time pressure. It was found that the shortest time limits induced more route-based strategies of taking path segments in the environment used during the learning phase the previous day. However, this behavior could be considered a task demand rather than a change in behavior due to the influence of stress necessarily.

Recently, Ruginski, Stefanucci, and Creem-Regehr (2018) asked participants to breathe through a small straw functioning as a method of hyperventilation to induce stress or feeling of anxiousness. Next participant were passively shown a video of a route through an environment. Finally, participants were asked to make pointing judgments. This procedure was carried out twice. There was no main effect on condition (anxiety vs control), however it was shown that females performed worse in the stress condition.

Interestingly, in a non-navigational spatial memory task, Schwabe et al. (2007) found that a group of stressed participants relied on a stimulus response strategy when their spatial memory is tested. In this study, they compared one group of participants stressed using the Trier Social Stressor Task to an unstressed control group. Participants then saw a series of dioramas (i.e., small-scale rooms set-ups) in which there were landmarks on the walls (e.g., door, clock, etc), a plant in one corner, and four cards placed on a table in the center of the room diorama. One of the four cards was a "win" card and the location for that card was the same relative to the three non-win cards on each of the twelve trials. On each trial, the participants were given three chances to find the win card. Here, participants could adopt one of two strategies. The first strategy requires learning where the card is in relation to the moving landmarks in the diorama (spatial strategy) and the other requires learning that the card was always directly near the plant object (response strategy). On the final trial (of 13), the plant object was disambiguated from the win card and thus reveals someone's strategy. In

this study, stressed participants adopted the stimulus-response learning strategy more than did the unstressed control participants. Although this is not a navigation task *per se*, it illustrates that spatial memory strategies—of which there are several in navigation tasks and analogous—can be influenced by stressors.

However, van Gerven, Ferguson, and Skelton (2016) found that participants rely on an allocentric (that is, an environmentally derived strategy rather than egocentric or selfrelated) strategy requiring complex environmental knowledge known to require some form of hippocampal activation. In this study, half of the participants were introduced to a paced auditory serial addition task as a stressor. This task requires the addition of interleaving numbers presented in a group in short succession by a computer out loud. When presented with 5, 1, 2, 3, the responses would be 6, 3, 5. The list of number would be held in memory while also calculating. Each of four blocks required a faster pace (2.4s down to .9s). The unstressed group was neither paced nor required to remember numbers as they were presented after each individual addition solution. After participants completed the task, they were placed in a virtual version of the Morris Water Maze (VMWM) in which they learned the location of a hidden platform in the arena. Then, to determine their strategy at test, they were able to navigate to a hidden platform by large distal landmarks viewed through windows of the arena or by the location of a single fixed cue near the hidden location during learning. This previously fixed cue was moved at test to the opposite quadrant. If participants navigated to the quadrant near the location of that now-moved object, they were navigating egocentrically. If they navigated via the distal landmarks, they were using an allocentric strategy. Relative to unstressed control participants, the stress group showed elevated heart rate, skin conductance, and blood pressure, however there was no significant difference

between groups in cortisol response. Interestingly, stressed participants navigated more by allocentric than by egocentric cues in the Virtual Morris Water Maze task. This unexpected result may have arisen because the stressor facilitated performance in this task by activating the hippocampus for optimal function rather than inundating it. In essence, all participants were at the top of the inverted U curve.

Two other studies have used the virtual version of the Morris water maze task in the context of stress and navigation on the side of learning. Duncko, Cornwell, Cui, Merikangas, and Grillon (2007) used the cold pressor task to evaluate behavior in the virtual version of the Morris water maze task. In this study, participants submerged their arm in near freezing water before learning and testing in the Morris water maze. They found better performance in the stressor group (number of successful trials and lower heading error) compared to a control group. Klopp, Garcia, Schulman, Ward, and Tartar (2012) argued that social stressors would not show this same pattern in virtual Morris water maze and even argued for a null result between conditions. In their study, participants performed the Trier social stress task or were assigned to the control condition. These researchers found no significant differences between conditions despite large differences in cortisol.

Further, other work has found effects of stress in various navigation tasks but only in certain participant sub-groups or tasks. In an early study concerning psychological stress and navigation, Thomas, Laurance, Nadel, and Jacobs (2010) induced stress via the Trier Social Stressor Task (cf. Kirschbaum et al., 1993), then after some delay participants were asked to traverse the virtual arena searching for blue squares that were visible (landmark navigation) and invisible (place navigation). The results of this study indicated that only stress group females produced reaction time latencies that were longer than the other three groups of

stressed males, and unstressed males and females. Similarly, Richardson and VanderKaay Tomasulo (2011) compared control participants to participants stressed via the Mirror Star Trace Task in which participants view a star on a mirror and trace the outline of it. In their spatial task, participants learned three paths in a virtual environment with several targets on each path. After walking each path participants then made directional judgments between objects from the start of the path they had learned. First, the stressor manipulation was not found to increase cortisol levels relative to the control group. Despite this, however, the stress group produced slower pointing responses to learned targets but no pointing accuracy difference was found between these groups. Therefore, the lack of pointing accuracy effects in this study could be explained by the lack of difference in measured salivary cortisol between groups as a function of an inadequate stressor task. Finally, Crede, Thrash, Hölscher, and Fabrikant (2019) used a pointing task in the presence or absence of time pressure after learning a virtual environment and also found no significant differences between groups.

In summary, when put under stress in the lab and given a spatial task, various results emerge. Meng and Zhang (2014) found that emergency egress is more difficult with simulated fire and smoke than matched controls. Duncko et al. (2007) found facilitating effects of the cold pressor stressor on navigation, while Klopp et al. (2012) found no effect of a social stressor on navigation. van Gerven et al. (2016) found that stressed participants relied on allocentric navigational cues more the control participants, but Schwabe et al. (2007) showed that stress increased the likelihood of using a stimulus response strategy. Ruginski et al. (2018) and Thomas et al. (2010) found that only females were negatively impacted by stress, in different navigation tasks and using different stressors. Interestingly, Brunyé et al.

(2016) found evidence that time pressure during navigation trials led to reliance on previously travelled routes.

The literature reviewed above points out that stress has some influences on memory for spatial tasks in humans and rats. However, especially within the human literature, there has not been sufficiently converging evidence. These mixed effects could be explained by several factors: types of participants, types of tasks, types of stressors and their administration. First, while the rodent is one animal model for testing hypotheses about human level cognition, it is not necessarily the case that rodent results extend to humans completely. Next, it is also possible that the tasks used with rodents do not approximately match tasks carried out by humans in real life. It is important to recognize the Morris Water Maze is not easily transferred to a human task, even in virtual reality. Many of the task parameters that makeup the Morris Water Maze, such as being wet, cold, annoyed, and scared, fall away when tested in VR. Thus, it is possible that these results cannot extend to humans.

Further, when considering the effects of stress on spatial memory, and navigation in particular, it is important to keep the task as realistic as possible. Several of the studies reviewed above did this well (Brunyé et al., 2016), whereas others did not (Thomas et al., 2010). Another important issue facing the research reviewed above is the stressor itself. As seen in Table 2, several studies above used the most effective type of stressor in the human literature, the Trier Social Stressor Test, whereas others did not. This may be critical in explaining the null effects found in other studies; however, this stimulates the idea that different stressors should be evaluated in the context of navigation performance. Finally, perhaps the most important issue that has led to various results in the research above is when

the stressor is presented relative to retention testing. Work in spatial and word-list learning tasks indicate that the placement of the stressor is important (de Quervain et al., 1998; de Quervain et al., 2000). Stressors were not always presented prior to the retention test, but rather before learning (Thomas et al., 2010; van Gervan et al., 2016; Richardson & VanderKaay Tomasulo, 2011) or were administered concurrently with the testing (Brunyé et al., 2016; Meng & Zhang, 2014).

In sum, there is strong evidence that stress can be detrimental towards memory retrieval, but the effects of stress on human spatial memory have not been adequately elucidated. Hence, there is a need to systematically study the effects of stress on navigation and how it could be mediated by cortisol.

In the work produced so far, stressors have not been optimally placed in order to draw out the effects acute stress may have on humans in a navigation task. A problem with some of the earlier studies is that they did not take account of the fact that the stress response in humans takes about 15 minutes for full reactivity to be achieved (Kirschbaum $\&$ Hellhammer, 1989). Thus, careful consideration must be taken when placing a stress protocol into an experimental task. For instance, although ecologically valid, using online stressors such as time pressure may produce a phase shift between the stress response and retention testing, in which the task has started but the body does not show elevated cortisol until midway through the task, thus underestimating any effect.¹ In this same way, building egress may not even be influenced by cortisol unless escape takes longer than 15 minutes. It is necessary is to place stressors prior to retrieval as has been accomplished in studies concerning word-list declarative memory. Placing the stressor prior to retrieval will establish

¹ Time pressure has not historically been shown to increase cortisol levels reliably (Dickerson and Kemeny, 2004).

whether navigation strategies differ as a function of stress.

Finally, an examination of various types of stressors should be evaluated in order to understand the stress-memory mechanism in human navigation. Social stressors may elicit cortisol but produce decontextualized effects in relation to a non-social navigation task. A more ecological approach may be to use a physical stressor, which might provide a contextualized stressor and thus alter navigation behavior and strategy in a different way. The question is whether or not the mechanism of the stress-dependent memory effect is due to any release of cortisol or combined effects of cortisol and other stress hormones such as the catecholamines.

In this dissertation, I aim to evaluate the effects of acute stress on strategy in a navigation task. To do so, I will use three stressors to examine their effects in a stressed condition and an active control condition, which will be counterbalanced. Two stressors are well-known (cold pressor and Trier Social Stress Test) and the third (cognitive fatigue) is an as-of-yet unexamined stressor task. In general, the expectation is that stress, via cortisol, will affect navigation strategy selection in the Dual Solution Paradigm task.

III. Two Experiments Establishing Equivalence of Two Maze Environments

The original research that introduced the Dual Solution Paradigm using a virtual environment indicated individual differences in route selection such that some participants rely on learned routes, some use on shortcuts, while most participants utilized both shortcuts and learned routes during the course of testing (Marchette et al., 2011). In line with previous research (Iaria et al., 2003), Marchette et al. (2011) showed that route selection in a novel virtual environment is related to individual differences in brain activation such that those who used well-learned routes showed more caudate activations and participants that navigated by shortcuts indicated more hippocampal activations. This paradigm allows for a reliable look at what strategies people use to navigate. Each participant's trials in the DSP can be coded for being on shortcuts, learned routes, reversals of the learned route, wandering, or a failure to reach the goal (Boone, Gong, & Hegarty, 2018). Further, distance and time travelled on each trial and path efficiency can be measured to assess efficiency.

In order to understand how people navigate under stress, it is necessary to also compare how people navigate in a control, unstressed context with their behavior during a stressful context. Therefore any experiment testing both conditions would need at least two different but functionally equivalent mazes such that one is not easier than the other for unanticipated reasons. The first two experiments in this dissertation focus on developing and comparing navigation strategy behavior in two environments. The original DSP maze developed by Marchette et al. (2011) was adopted here. To create a second maze, the original maze was mirrored on the *y*-axis. These mazes differed in superficial visual characteristics (such as the color of bricks on the walls) and I will refer to them as the red-brick and gray

brick environments. Experiment 1a compares behavior in these two mazes. Experiment 1b utilizes a larger sample balanced for gender. To anticipate, the two mazes are similar in outcome measures despite a trend for more efficient navigation during the second session of navigation trials.

Experiment 1a: Red Brick Maze versus Gray Brick Maze

The goals of Experiment 1a were to: 1) build two versions of the DSP in house, 2) replicate previous DSP results with both mazes, in order to 3) compare the two mazes on strategy and efficiency measures, and finally 4) determine the most diagnostic trials for future research.

In this experiment, participants learn and are subsequently tested in one version of the DSP maze. Following a break period of approximately five minutes participants are tested in a second, but different DSP maze. This design was used in order to address two basic research questions: 1) are the two mazes equivalent on outcome measures of strategy and efficiency? and 2) how much improvement is seen from one environment to the other as a function of practice on the task?

Participants

Participants were 16 (10 females) University of California, Santa Barbara undergraduates who participated in return for course credit. Four total participants were excluded from analysis either due to motion sickness ($n = 2$) or English proficiency ($n = 2$), leaving 12 participants in the final sample.

Design

A 2 (maze: Red Brick vs Gray Brick) x 2 (Order: Red-Gray vs Gray-Red) mixed subjects design was used. Maze was within subjects and order was between subjects. The ratio of males to females was held constant across maze type.

Materials

Maze development. Maze and trial development were undertaken in a systematic manner in order to ensure equivalency between mazes in a number of dimensions specifically: the number of steps on the learning path, number and type of objects within the mazes, and the distance to be travelled across trials on the learned route or the shortcut. Each environment was initially constructed in Blender (a free, open source software toolset to create 3d objects) and then imported into Unity3d. These mazes were constructed as an 11 x 11 grid of unit squares. Object location alcoves were extruded into the wall at a depth of half of a unit square. In this way, the amount of squares, or "steps," traversed by a participant on a given trial can be counted (see Figure 2).

Figure 2. Maze layouts used in this experiment representing the learned route (dashed line) and environmental view of the participants. Participants learn only this route in each maze. a) Red brick maze schematic structure modeled after Marchette et al. (2011), b) Gray brick maze schematic mirroring the red brick maze, c) participant view of Red brick maze and d) Gray brick maze during the learning phase taken from the same viewpoint. *Note*. Black diamonds represent local landmark locations. Participants walk this route five total times in first person perspective on a desktop computer in the learning phase.

As can be seen in Figure 2a, the red brick maze schematic was taken directly from Marchette et al. (2011) without modification of the environmental structure despite differences in textures and objects. The gray brick maze (Figure 2b) was created by mirroring the red brick maze along the y-axis and then placing the starting point in a different location. Secondly, the texture of the walls was changed in each maze to further suggest a change of environment. In the red brick maze, the walls consist of red brick (Figure 2c) while gray bricks were used in the gray brick maze (Figure 2d). The floor texture (basic light gray speckled asphalt) and sky (basic light blue, no single salient light source) was unchanged between the environments. A training maze was also created in order to allow participants

time to understand the keyboard (movement) and mouse (heading) navigation controls before starting the task. This maze was the same size and shape as the other mazes and the walls were textured using the red brick. Inside of the training maze, there were four square pylons arranged in a 2 x 2 grid which allowed for walking around the pylons.

In the red brick maze, the order of the objects alcoves along the learning tour were as follows: a brown desk chair, a blue U.S. Post Office mail drop box, a multicolored telescope, a large potted plant, a picnic table, a stove, a piano, a trashcan, an empty bookshelf, a wheelbarrow, a harp, and a wooden wishing well. In the gray brick maze, the order of the objects were: a desk, a water cooler, a streetlamp, a red stepladder, a refrigerator, a bicycle, a lion statue, a couch, a phone booth, a wooden swing, a grandfather clock, and a television. All objects were available for free download from Turbosquid.com or through the Unity asset store.

Trial selection. Trials for the task were selected in order to ensure that a shortcut was sufficiently beneficial compared to the learned or the reversal of the learned route on each trial. In order to do this, the number of steps (grid squares) between each pair of locations was counted, in the forward and backward directions on the learned route. Next, to determine the usefulness of a shortcut that someone might use on a given trial, a savings score was computed by the following equation:

Savings Score = (Learned Route steps – Shortcut steps) / Learned steps (Eq. 1) For each of the possible trials, this value indicates how much savings a particular shortcut allowed relative to the learned route between any two locations. Individual trials with savings scores of less than or equal to 25% were not included. Further, to ensure that participants did not overlearn any section of the maze, each of the object locations was used twice as the

starting point of a trial and twice as the ending point of a trial. This left a total of 24 trials to be used in evaluating participant navigation behavior. The shortcut in these trials also had at least a 19% savings compared to route reversal. The average savings across all trials was 51%. Given that the red brick maze and the gray brick maze are mirror reflections of each other, the trials in each maze are the same except mirrored. All possible trials can be found in Appendix A.

DSP strategy trial coding system. A trial coding system was established in earlier research (Boone, Gong, & Hegarty, 2018). First, success to reach the goal within the 40s time limit was used as a measure of task performance. Next, as a measure of strategy, each trial is coded strictly based on the route taken as following the learned route, taking a shortcut, reversing the learned route, or wandering (crossing over their own route) as a measure of strategy. However, some trials could not be *strictly* coded as any of these. For example, a participant, on a given trial, might have primarily followed the learned path but near the target landmark had a minor deviation from this path, thus this trial is not fully on the learned route nor the strict shortcut. These trials were categorized using a liberal coding scheme as follows: a liberal shortcut was defined as a path that is no more than 84% the length of the learned route *and in which* less than 70% of the path taken was on the learned route. A liberal learned route was coded if participants traversed 70% or more of the learned route. Similarly, trials coded as reversing the learned route overlapped this route by at least 70%. Trials were classified as "wandering" when a major section of the participant's route was repeated, so that the route taken was longer than the learned route. Finally, trials were classified as uncodable when the route taken was greater than 84% of the length of the learned route *and* less than 70% on the learned route. Figure 3 shows these categories.

Figure 3. Representative examples of each major category code on the same trial in the DSP. *Note*. a) shortcut, b) shortcut liberal, c) learned, d) learned liberal, e) reversed learned, f) reversed learned liberal, g) uncodable (and retracing), and h) wandering. The purple line indicates the entire learned path. The yellow line indicates the shortcut path on this specific trial. The black line represents navigation path of the participant. The green and red rectangles represent the start and end location on this trial, respectively. Participants did not see this colored start or end colored squares.

Dependent variables of the DSP. Coded trials were condensed into a single, solution

index measure (SI; Furman et al., 2014; Marchette et al., 2011) but modified for other

navigation routes used, given by the following equation (henceforth known as Solution

Index):

Solution Index = Sum of Shortcut Trials / Successful Trials
$$
(Eq. 2)
$$

This formula produces a number on a scale of 0 (indicating all non-shortcut routes) to 1

(indicating all shortcuts). Three efficiency variables were calculated. First, measures of (1) time and (2) distance travelled on each trial assessed by averaging time and distance across trials. In addition, a measure of path efficiency was computed by dividing the distance traveled per trial by the optimal (i.e., shortest) distance between the two locations (See Equations 3 and 4).

Path Efficiency per Trial = Distance traveled / Shortest distance between locations (Eq. 3)

Average Path Efficiency = \sum (Path Efficiency per Trial) / Number of Trials (Eq. 4) This creates a metric that expresses the number of shortcut path length traveled, on average (e.g., if path efficiency equals 2 then the average path efficiency is two times the optimal path length).

Self-report Measures. The materials included the following self-report measures. The Santa Barbara Sense of Direction Scale (SBSOD; Hegarty et al., 2002) is a self-report measure of environmental spatial abilities. Participants are provided fifteen statements such as "I tend to think of my environment in terms of cardinal directions (N, S, E, W)" and rate their agreement with each on a scale of 1-7 in which 1 is "strongly agree" and 7 is "strongly disagree." The SBSOD scale is presented in Appendix B. The Pazzaglia Scale (QSR; Pazzaglia et al., 2000) is a 11-item scale which asks participants to consider various aspect of their large scale spatial ability including a series of questions about their sense of direction and about how they approached navigation in a personally derived context (e.g., a recent trip). A 1-5 scale is provided where 1 is "not at all" and 5 is "very much." Several subscales are produced through this questionnaire including two subscales focusing on sense of direction, use of cardinal directions and landmarks, as well as survey and route strategies. The QSR scale is presented in Appendix C.

Apparatus

This experiment was administered using a Dell XPS 8920 computer running Windows 10 64-bit and with a GeForce GTX 1070 graphics card presented through Unity 3D software. The environment was displayed on a 27-inch LCD monitor with a refresh rate of 60hz at a resolution of 1920 x 1080. The viewing distance was approximately 1000mm.

Procedure

Participants gave informed consent prior to participation. First, participants were introduced to the virtual environment displayed in first person perspective on the computer monitor. Next, they were given the opportunity to practice with the active navigation controls (keyboard and mouse) within the training maze until they indicated they were comfortable with the controls. In the learning phase, participants were asked to follow red arrows on the ground to navigate the maze (Figure 2c and 2d), while taking note of the objects that they passed. An invisible wall blocked each corridor that was not on the learned path, but the view of the corridor was not obscured. Participants followed the route a total of five times. While walking the learning tour the first time, the participant said the name of each object aloud. Participants were corrected when they were incorrect. The final four encoding tours were completed on their own. Following a 30 second break participants were given instructions for the testing phase. Participants were placed in different locations along the learned route and were asked to navigate to another location within the maze. For example, as is presented in Figure 3, in one trial the participant was placed near the wooden well and had to navigate to the stove. For this trial, the instructions were presented verbally as follows: "Please navigate to the [object]" where object was the goal location for that specific trial. There were 24 total trials presented in random order. Upon reaching the goal location or when 40s elapsed, the

trial ended, a light blue screen said "Please wait for the next trial" for 1.5s. Upon seeing the environment again, they were in the next starting location (all instructions can be found in Appendix D). After all 24 trials, participants were given a five minute break in which they could use the restroom and were provided with a small can of soda or water. Next, they were placed in the second maze and repeated the process: learn the route five times and complete 24 trials.

Finally participants were administered the SBSOD, the QSR, and a short demographics questionnaire. After completion of all tasks, participants were debriefed and dismissed.

Results

The plan for this results section is to present a comparison of the two mazes on each DV (solution index and efficiency), the correlation between solution index on the two mazes, as well as present data concerning diagnostic trial selection for future experiments.

DSP DVs. As seen in Table 3, successful navigation to the goal location occurred on 93% of the trials within the 40-second time limit (Mean time $= 24.11$ s, SD $= 9.04$). A strict coding of the main strategies (shortcut, learned route, reversal of learned route, wandering) accounted for 52% of all trials, while the liberal coding accounted for 37% of the trials (11% of trials were uncodable).

In terms of individual differences, as seen in Figure 4, across both mazes, participants showed a wide range of strategy preference from nearly all learned routes to all shortcuts (Red brick maze Range of SI = .04 to .71; gray brick maze Range of SI = .07 to .67) as in previous research on this task (Marchette et al., 2011; Furman et al., 2014).

| | Red Brick Maze First | | Gray Brick Maze First | | | |
|-----------|-----------------------------|-------------|-----------------------|------------|--|--|
| | Red Brick | Gray Brick | Gray Brick Red Brick | | | |
| Shortcut | 4.67(2.58) | 6.00(2.97) | 8.00(5.69) | 8.33(5.39) | | |
| Learned | 9.33(3.88) | 8.83 (5.85) | 6.67(4.76) | 7.50(5.75) | | |
| Reversal | 4.67(1.87) | 4.00(2.45) | 2.17(1.94) | 2.83(2.40) | | |
| Wandering | 1.00(1.10) | 0.67(0.52) | 1.17(1.84) | 1.00(0.63) | | |
| Uncodable | 1.33(1.75) | 2.33(2.25) | 3.67(2.42) | 3.00(2.37) | | |

Table 3. Average number of trials out of 24 coded as each route selection by maze (red brick vs gray brick) and order in which they completed the two maze tasks. Standard deviations are presented in parentheses.

Navigation Performance. Using a 2 (maze type) by 2 (order) ANOVA on the number of successful trials, success in the two mazes was not significantly different, $F(1,10) = .02$, *p* = .89. Further, a main effect of order of the mazes was not significant, $F(1,10) = .16$, $p = .70$. Finally, no interaction was found between maze type and order, $F(1,10) = 1.53$, $p = .25$.

 Figure 4. Scatterplot of Solution Index measures from the red brick maze and the gray brick maze indicating high similarity of strategy behavior.

Navigation Strategy. Using a 2 (maze type) by 2 (order) ANOVA to analyze the number of times each strategy was used, there were no main effects of maze type, order, nor any interactions between these variables for any of the strategies (shortcut, learned, reversals, wandering, uncodable), all $F(1,10) \le 1.36$, all $p \ge 0.36$. Descriptive statistics of route selection behaviors can be found in Table 3.

As can be seen in Figure 4, there was a strong correlation between the two mazes in terms of solution index, $r(10) = .78$, $p = .003$. Further, there was one outlier that took only one shortcut in the gray brick maze and removal of that outlier increased this correlation, $r(9)$ $= .98, p < .001$. A 2 (maze) x 2 (order) ANOVA using solution index as the dependent variable indicated no difference between mazes, $F(1, 10) = .50$, $p = .50$, and no main effect of maze order, $F(1, 10) = .85$, $p = .38$. Finally, there was no interaction between maze and order, $F(1, 10) = .89$, $p = .37$. Table 4 presents descriptive statistics for solution index.

Table 4. Descriptive statistics objective measures by maze (red brick vs gray brick) and order in which they completed the two maze tasks. Standard deviations are presented in parentheses.

| | Red Brick Maze First | | Gray Brick Maze First | | |
|-----------------|-----------------------------|----------------|-----------------------|----------------|--|
| | Red Brick | Gray Brick | Gray Brick | Red Brick | |
| Success | 21.83(1.17) | 22.50(1.87) | 22.00(1.67) | 22.83(1.17) | |
| Solution Index | 0.21(0.11) | 0.27(0.14) | 0.36(0.23) | 0.36(0.23) | |
| Time | 26.28(3.03) | 24.10 (2.66) | 23.57(3.32) | 22.53(3.14) | |
| Distance | 405.66 (34.72) | 384.54 (39.27) | 371.87 (72.89) | 358.27 (66.97) | |
| Path Efficiency | 2.71(0.27) | 2.34(0.42) | 2.41(0.47) | 2.53(0.39) | |

Note. Success is out of 24. Time was measured seconds. Distance was measured in Unity units (roughly meters). Path efficiency was measured in shortcut distances at the trial level $(e.g., 2.00 = travel 2x longer than the shortcut).$

Navigation Efficiency. Using a 2 (maze) x 2 (order) ANOVA on distance efficiency data, no difference was found between mazes, $F(1, 10) = .16$, $p = .70$, nor was there a main effect of maze order, $F(1, 10) = .94$, $p = .35$. Finally, there was no interaction between maze and order, $F(1, 10) = 3.35$, $p = .10$.

Further, no difference was found between mazes in time efficiency, $F(1, 10) = 1.20$, *p* $= .30$, nor was there a main effect of maze order, $F(1, 10) = 1.63$, $p = .23$. However, there was an interaction between maze and order, $F(1, 10) = 9.60$, $p = .01$, such that the participants in the Red-Gray order were faster on the second maze (*∆time* = 2.18s) than participants in the Gray-Red order (*∆time* = 1.04s). This effect may be due to differences in between the groups assigned to each condition order.

In terms of path efficiency, there was no main effect of maze type, $F(1, 10) = .40$, $p =$.54, nor was there a main effect of maze order, $F(1, 10) = 1.39$, $p = .27$. Finally, there was no interaction between maze and order, $F(1, 10) = 2.42$, $p = .15$.

Finally, Table 5 shows correlations across all three measures within each session. As can be seen, these measures are highly correlated.

| | Red Brick Maze | | | Gray Brick Maze | | | |
|----------------------------|-----------------------|-------|---------------------|-----------------|----------|---------------------|--|
| | Time | | Distance Efficiency | Time | | Distance Efficiency | |
| Red Brick Time | | 85*** | $83***$ | $74**$ | .54 | .54 | |
| Red Brick Distance | | | $96***$ | 74** | $.80**$ | $.70**$ | |
| Red Brick Efficiency | | | | $.68*$ | $75**$ | $71**$ | |
| Gray Brick Time | | | | | $.86***$ | $.81**$ | |
| Gray Brick Distance | | | | | | $.90***$ | |

Table 5. Correlations of efficiency measures in Experiment 1a across each maze type. Red Brick Maze Gray Brick Maze

Note. $df = 10.$ *** $p \le 0.001$, ** $p \le 0.01$, * $p = 0.02$.

Diagnostic Trial Selection. To determine the set of most diagnostic trials, each trial for each maze was evaluated based on the proportion of trials that were categorized as shortcut or learned out of all trials. Trials were discarded if in both mazes the proportion of categorizable trials was less than 42%, based on all coding. This analysis left 20 total trials for later use, representing the most diagnostic trials. Confining the above analyses to these 20 trials does not appreciably change the results.

Discussion

The major goals of Experiment 1a were to build a new version of the DSP, replicate earlier findings, and equate two mazes for future research. The results presented here indicate a successful replication such that participants showed a range of route selection behaviors in both DSP environments. The main result of this experiment is that performance and strategy choice was not shown to be different between the mazes (red vs gray brick) and there was a high correlation between the solution indices for the two mazes.

Finally, when using only the 20 most diagnostic trials, the results were highly similar. Taken together, these results indicate general equivalence between the red brick maze and gray brick (mirrored) mazes. Therefore, these two mazes can be used in later studies in which two environments are needed.

Experiment 1b: Two Mazes with Larger Sample and Fewer Trials

Although Experiment 1a indicated that two mirrored mazes were equivalent in terms of all DSP DVs, the sample size was small and mainly sampled females. Given that the DSP has shown gender differences in performance (Boone et al., 2018), Experiment 1b utilized a larger sample consisting of equal males and females, using the 20 most diagnostic trials derived from Experiment 1a. As in Experiment 1a, participants learned in one maze and were tested on 20 trials followed by the same procedure in the second maze. One prediction is that no differences will be found between the two mazes in terms of solution index or efficiency. Finally, the effects of repeated task exposure will be evaluated. It is possible that repeated task exposure may lead to more shortcutting over time.

Participants

Participants were 42 (22 females) University of California, Santa Barbara undergraduates who participated in return for course credit. Two female participants were excluded from analysis due to motion sickness. A final sample of 20 males and 20 females was used for all analyses.

Design

A 2 (maze: Red brick maze vs Gray brick maze) x 2 (maze order: Red-Gray vs Gray-Red) mixed design was used.

Methods

All materials and methods were equivalent to Experiment 1a except the use of only 20 trials. In brief, all participants learned and navigated in two mazes, with order counterbalanced across participants.

Results

The plan for this results section is to compare the two mazes on each DV (solution index and efficiency) across each session of the task and examine the correlation between the solution indices for the two mazes.

DSP DVs. Successful navigation to the goal location occurred on 87% of the trials in Session 1 and 88% of the trials in session 2 within the 40-second time limit (Mean time Session $1 = 24.35$, $SD = 4.01$; Mean time Session $2 = 23.08$ s, $SD = 4.49$). A strict coding of the main strategies (shortcut, learned route, reversal of learned route, wandering) accounted for 54% of all trials, while 35% were coded as using liberal routes and 11% were uncodable. The final categorization of trials is shown in Table 6 across orders.

Table 6. Average number of trials out of 20 coded as following each strategy by maze (red brick vs gray brick) and order in which they completed the two maze tasks. Standard deviations are presented in parentheses.

| | Red Brick Maze First | | Gray Brick Maze First | | |
|-----------|-----------------------------|------------|-----------------------|------------------|--|
| | Red Brick | Gray Brick | Gray Brick | Red Brick | |
| Shortcut | 5.30(3.10) | 7.60(4.02) | 5.20(3.41) | 4.45(3.53) | |
| Learned | 6.20(3.02) | 4.60(3.50) | 8.35(5.37) | 7.80(5.60) | |
| Reversal | 2.80(1.91) | 2.00(1.52) | 2.15(1.60) | 2.85(1.90) | |
| Wandering | 0.45(0.76) | 0.30(0.66) | 0.55(0.89) | 0.50(0.69) | |
| Uncodable | 2.20(1.99) | 2.80(1.51) | 1.50(1.79) | 2.20(1.77) | |

In terms of individual differences, as seen in Figure 5, across both sessions, participants showed a wide range of strategy preference from nearly all non-shortcut routes to mostly shortcuts (Red brick maze Range of $SI = .00$ to .58; Gray brick maze Range of $SI =$.00 to .75 respectively) as in Experiment 1 and previous research on this task. Importantly,

there was positive correlation between the two sessions, $r(38) = .45$, $p = .004$, indicating participants largely used the same strategy between sessions. Note, this correlation is particular to session, in which maze type is counterbalanced.

Figure 5. Scatter plot of Solution Index measures from both mazes regardless of session indicating high similarity of strategy behavior.

Navigation Performance. A 2 (maze) x 2 (order) ANOVA using navigation success count as the dependent variable indicated that success rates in the two mazes were not significantly different from each other, $F(1,38) = .15$, $p = .70$. Further, there was no main effect of order of the mazes, $F(1,38) = .96$, $p = .33$. Finally, no interaction was found between maze type and order, $F(1,38) = .26$, $p = .61$.

Navigation Strategy. As can be seen in Figure 5, there was a strong correlation between the two mazes in terms of solution index, $r(38) = .48$, $p = .002$. Further, there was one outlier that did not take any shortcuts in the red brick maze and removal of that outlier increased this correlation, $r(37) = .59$, $p < .001$. Note that this correlation is across maze type, rather than session.

Using a 2 (maze) x 2 (order) ANOVA on solution index data, participants took more

shortcuts in the gray brick maze ($M = .36$, $SD = .21$) relative to the red brick maze ($M = .28$, *SD* = .18) on solution index, $F(1, 38) = 6.89$, $p = .01$, $\eta_p^2 = .15$. The main effect of maze order was trending towards significance, $F(1, 38) = 3.65$, $p = .06$, suggesting more shortcuts taken when given the gray brick maze second, whereas shortcutting behavior was similar in the gray to red maze order. However, no interaction between maze and maze order was found, $F(1, 38) = 1.70$, $p = .20$. Descriptive statistics of route selection behaviors can be found in Table 7.

Table 7. Descriptive statistics objective measures by maze (red brick vs gray brick) and order in which they completed the two maze tasks. Standard deviations are presented in parentheses.

| | Red Brick Maze First | | Gray Brick Maze First | | |
|-----------------|-----------------------------|----------------|-----------------------|----------------|--|
| | Red Brick | Gray Brick | Red Brick | Gray Brick | |
| Success | 16.95(2.35) | 17.30(2.25) | 17.80(2.35) | 17.75(2.75) | |
| Solution Index | 0.31(0.17) | 0.43(0.21) | 0.30(0.18) | 0.26(0.19) | |
| Time | 24.34 (3.97) | 22.77 (4.80) | 24.38 (4.15) | 23.40 (4.25) | |
| Distance | 379.57 (59.33) | 360.67 (81.82) | 391.74 (73.07) | 382.72 (61.59) | |
| Path Efficiency | 2.46(0.47) | 2.41(0.55) | 2.62(0.44) | 2.58(0.47) | |

Note. Success is out of 20. Time was measured seconds. Distance was measured in Unity units (roughly meters). Path efficiency was measured in shortcut distances at the trial level (e.g., 2.00 = travel 2x longer than the shortcut).

Navigation Efficiency. Descriptive statistics for each measure can be found in Table 7. A 2 (maze) x 2 (order) ANOVA using distance efficiency as the dependent measure indicated no difference was found between mazes, $F(1, 38) = .20$, $p = .62$. There was neither a main effect of maze order, $F(1, 38) = .82$, $p = .37$, nor and interaction between maze and order, $F(1, 38) = 1.55$, $p = .20$.

A 2 (maze) x 2 (order) ANOVA on *time* efficiency indicated no main effect of

session, $F(1, 38) = .23$, $p = .63$. There was there no main effect of maze order, $F(1, 38) = .08$, $p = 0.78$. However, there was an marginally significant interaction between maze and order, $F(1, 38) = 4.18$, $p = .05$, $\eta_p^2 = .10$. Simple effects indicated no significant differences between the orders, both $F(1, 38) = 3.19$, $p = .08$. That is, comparing the mazes across the order of the task did not show significant differences.

Finally, using a 2 (maze) x 2 (order) ANOVA on path efficiency data, no difference was found between mazes, $F(1, 38) = .01$, $p = .91$. There was neither a main effect of maze order, $F(1, 38) = 1.97$, $p = .17$, nor and interaction between maze and order, $F(1, 38) = .24$, *p* = .63. As seen in Table 8, efficiency measures were highly correlated. Of particular note is that the correlations of across measures within session are large.

| | Red Brick Maze | | | Gray Brick Maze | | |
|----------------------------|----------------|----------|------------|-----------------|----------|------------|
| | Time | Distance | Efficiency | Time | Distance | Efficiency |
| Red Brick Time | | $.84***$ | 49*** | $.55***$ | .29 | .16 |
| Red Brick Distance | | | $.71***$ | $.45**$ | $.49***$ | $.38*$ |
| Red Brick Efficiency | | | -- | .15 | .29 | .24 |
| Gray Brick Time | | | | -- | $.80***$ | $.62***$ |
| Gray Brick Distance | | | | | -- | $.85***$ |

Table 8. Correlations of efficiency measures in Experiment 1b across maze type.

Note. $df = 38.*** p \le .001,*** p \le .01,* p = .02.$

Discussion

Experiment 1b indicated that the two mazes produced similar results on the success and efficiency measures, regardless of order. There was a significant trend for participants to take more shortcuts in the gray-brick maze. This difference represents a difference of about two shortcut trials more in the gray-brick maze. However, it should be noted that this effect

seems to arise only in one direction, primarily when the gray brick maze is second and this could represent a session, or practice, effect than an effect of the maze per se. However, these effects may have arisen from unknown differences between the groups.

As in Experiment 1a, the measures of distance and path efficiency were highly correlated. Future analyses will eliminate distance and focus on path efficiency. It should be noted that the correlation between solution index values in the two mazes, as well as the correlations between efficiency measures, were weaker in this experiment than in Experiment 1a. However, overall, these results here are similar to Experiment 1a and suggest that the results arising from the two experimental mazes (red brick maze and the mirrored gray brick maze) are similar enough to be used for future testing in which two sessions are necessary.

IV. Assessing Navigation Strategy Switching Related to Three Experimental Stressors

As seen in Experiments 1a and 1b, as well as previous work (Marchette et al., 2011), there are substantial individual differences in navigation strategy. Some people prefer to take learned routes while others navigate more flexibly by taking shortcuts. The brain areas that support these types of navigation strategies have been investigated in work that has used the DSP in fMRI as well as other tasks that assess navigation strategies in other ways (Marchette et al., 2011; Furman et al., 2014). The hippocampus serves our flexible navigation strategies, while the caudate nucleus serves our well-learned route navigation system.

Interestingly, previous work has indicated that various types memory can be affected by stress. For instance, research has shown memory decrements for word lists after stress and in rodents memory for the location of a previously learned platform can be impaired when the rat experiences stressors 30 minutes prior to retrieval (de Quervain et al., 1998). This work suggests that a stressor may functionally block memory for locations within a layout, especially if someone is navigating by a cognitive map like (hippocampus dependent) strategy. This is perhaps because the hippocampus has many receptors for glucocorticoids such as cortisol (McEwen et al., 1968; Herman et al., 1989) whereas the caudate nucleus does not (Defiore, & Turner, 1983).

Given this, then, the following three experiments evaluate the effect of stressors on human navigation. The hypothesis is that introducing a stressor that elicits a large cortisol increase should produce selective deficits in performance in those navigators preferring to use the hippocampus-based place strategy. While the previous work regarding human navigation under stress have shown weak or no effects on spatial tasks (Richardson and

VanderKaay Tomasulo, 2012; Thomas et al., 2010; Crede et al., 2019; Klopp et al., 2012), and some have shown contradictory effects (Van Gervan et al., 2016; Duncko et al., 2007), at least two studies are consistent with the predicted effects. First, Brunyé et al. (2016) found that when participants were put under increasingly difficult time limits to reach goal locations, more learned routes were used while navigating. Although time pressure is not typically found to achieve large cortisol releases, this works indicates that participants may find it difficult to navigate flexibly under stress. Further, Ruginksi et al. (2018) found that artificially manipulating stress (or feelings of anxiety) using a breathing task can negatively influence performance on a pointing task, however, this effect was only found in female participants. In this case, the pointing task is a reflection of the quality of the mental representation of the learned space (i.e., the cognitive map). Therefore, participants were less able to access those memories during that task and this result is consistent with the current driving hypothesis.

With the exception of Brunyé et al. (2016), each study has induced stress before the learning process and none of these studies have focused on navigation in an environment from prior knowledge in order to extract navigation strategy measurements. In Experiments 2, 3, and 4, participants learn and are tested in two separate sessions. One session is a stressfree session while the second session is a stressful context. The order of session type (stress vs control) was counterbalanced. Two stressors known to elicit large cortisol releases were chosen. One stressor represents a physiological threat to the body (cold water), while the other represents a social threat to self (public speaking). A third stressor represents a mental fatigue or frustration task. The prediction is that navigation becomes less flexible while navigating under the stressor condition (less shortcuts taken, less efficient) relative to the

control condition as access to the hippocampally based cognitive map is restricted due to stress via cortisol. The key variables of interest will include solution index (navigation strategy), time and path efficiency measures, route retracing, initial movement time per trial, and dwell time (stopping behavior). Each of these variables may be influenced by the presence of stress during the task trials.

Experiment 2: Cold Pressor Task Stressor and Navigation Strategy and Efficiency

Physiological stressors are a class of stressors that produce a threat to the body which is in contrast to psychological stressors. Both stressor types can elicit cortisol, although the threat posed by each stressor may be cognitively evaluated in different ways. One physiological stressor task that has been widely used in the literature to reliably stress participants above baseline is the Cold pressor task (CPT; Hines & Brown, 1932). The CPT traditionally requires participants to submerge a hand or forearm in an ice water bath between 0° and 4° C for a period of up to three minutes. In some cases, the active control condition requires participants to place an arm in water at room temperature or slightly warmer (30- 38˚C). As can be seen from the previous work that has used the CPT (Table 1), cortisol levels are substantially elevated above baseline (~9 nmol/l on average) after CPT onset. Recent research has shown larger effects of cortisol action than the classic CPT when using bilateral foot submersion (Larra, Schilling, Röhrig, & Schächinger, 2015). Therefore, in the present experiment, participants are required to place both feet in the water bath. This methodology has the added advantage that hands and fingers are not made cold or immobile by the ice bath and thus can be used for immediate subsequent tasks. Given the relative effects of bilateral foot submersion on salivary cortisol and other peripheral physiological measures, it is perhaps the best first stressor to be employed to explore the effects of cortisol on navigation

strategy and performance.

The effect of stress on navigation performance and strategy has been studied in several methods including frustration stressors such as the mirror star tracing task (Richardson & VanderKaay Tomasulo, 2012) and time pressure (Brunyé et al., 2016). As of yet, no studies have yet tested the effects of physiological stress on humans navigating from prior knowledge. In one study, however, Duncko et al. (2007) evaluated participants learning *and* navigation memory retrieval after a bout of acute stress via the cold pressor task. Here they found that participants were more successful across trials and showed lower heading error compared to unstressed controls. Therefore, a question remains as to the effects of stress on navigating from prior knowledge.

In Experiment 2, navigation strategy was measured twice in the context of a larger study investigating stress and cognition using. During one session, participants navigated in the DSP after a series of 90s bilateral foot CPT sessions and on another day participants navigated in the DSP after placing their feet in warm water (order counterbalanced across participants). During both sessions physiological, eyetracking, and thermal imaging recordings were collected but will not be presented here.

It is predicted that if place, or cognitive map based navigation is disrupted by stress due to increased levels of cortisol in the hippocampus, then those participants expressing more shortcuts during the control session, will show fewer shortcuts during the CPT session. Further, the effect of stress could also be seen through measures of efficiency such as average time to find the target object per trial, the average path efficiency. Finally, other measures such as route retracing, initial movement time, and dwell time (stops) may indicate differences between sessions. It is hypothesized that if stress influence the navigation process

in general, people may need longer to think about a path to take (initial movement time; stops) but also may need to backtrack on already walked paths (retracing) while under stress.

Methods

Participants

Participants consisted of 48 University of California, Santa Barbara students (22 females) participating for 20 dollars per hour of their time. Two participants were dropped due to motion sickness. There were no differences between condition orders on SBSOD,

 $t(45) = 1.52, p = .13.$

Design

A 2 (stressor condition: Stressor vs Active Control) x (order: Control – Stressor vs Stressor-Control) design was used. Session and maze type were manipulated within subjects and order of sessions was counterbalanced. Order of conditions was manipulated between subjects.

Materials and Apparatus

All materials used to present this experiment were similar to the Experiment 1b with the following exceptions. First, the monitor used was an Asus VS278 27-inch monitor, the resolution was 1920x1080 with a refresh rate of 60hz at a resolution of 1920 x 1080. The viewing distance was approximately 1350mm. Matlab was used to initialize the program in order to start relevant recordings for physiology, eyetracking, and thermal imaging. In Experiments 1a and 1b, the screen images were passed directly to the testing monitor. In Experiment 2, however, the images were passed via a 2-port KVM switch, which allowed other computers to communicate with the testing monitor. Triggers, indicating event related information within the experiment (namely the start of each trial), were passed to the EEG

computer via a Labjack U3-LV device.

Thermo cyrotubes produced by Thermo Fisher Scientific were used to collect saliva at regular intervals across the testing sessions, which were marked with participant number, session, and sample number within the session. After collection, cryotubes were placed into a freezer at a temperature of -80˚C. Saliva samples were shipped on dry ice and assayed at the University of California Davis Clinical Endocrinology Lab using standard ELISA cortisol assay kits produced by Salimetrics, Inc.

A large, oval shaped metal washbasin was used for the cold pressor task, filled approximately 60% full with water. For the stress condition, ice was added to maintain a temperature between 0 and 4˚ C. For control conditions, the water was warmed to between 30 and 38 ˚C. The temperature was continuously recorded by a Zacro digital thermometer.

Other materials used were not necessarily related to the navigation portion of the experiment, however, they will be described here in brief. EEG data were recorded using a Brain Products ActiCHamp system (Brain Vision LLC, Morrisville, NC) with 64 electrodes embedded within an actiCAP elastic cap. Two electrodes were placed directly to the right and left mastoids in order to monitor blinking. Abralyt HiCl 1000gr gel was injected into each electrode to increase conductance for the electrode to pick up the signal from the scalp. The cap was connected to an amplifier produced by Brain Products, which was connected to a recording computer. Data were sampled at 500 Hz and referenced to the average mastoid signal. All impedances were \leq 15 kΩ. Participants were fitted with electrodes using NuPrep skin prep gel on their body at positions across their torso and lower neck used to measure their heart rate. The electrodes were EL-501 small stress electrodes produced by BioPac, Inc. Other physiological measures such as blood pressure was recorded through a Biopac module

onto a Dell Inspiron laptop.

An Eyelink T1000 eyetracker was used to record eye movements and record pupilometry during all tasks, which was recorded to a Dell desktop computer. A Flir A600 series thermal imaging unit was used to collect thermal images of the face during all tasks, recorded to a Macintosh computer.

Procedure²

This experiment was conducted in the context of a larger study that examine that effects of stress on several cognitive tasks. The overall procedure for the study can be seen in Figure 6 and consisted of five sessions which were preceded by a phone interview for the purposes of prescreening and an online questionnaire. The five sessions included a blood draw to assess baseline hormone levels, a VO2 max test, a baseline (no stressor) session, and two counterbalanced sessions of active control and stress conditions.

Figure 6. Overall process of the BOSS procedure.

² The navigation work concerned in the dissertation was embedded within a larger study seeking to understand the effects of stress on various cognitive functions. In this section, the overall procedure of the entire study will be described. However, only data relating to the main navigation task and saliva samples will be explored as part of this dissertation. It is important to note that every effort was taken to ensure that stress, should it be elicited by the cold pressor task, would be found during each cognitive task.

The prescreening phone interview included questions concerning medical history information that may disqualify someone such as heart conditions, BMI, medications, and ensuring that they would be comfortable enough with any potential stressor. A short description of each stressor was verbally described to them (See Appendix E). If accepted to the study, participant completed an online questionnaire concerning demographics, and other health and cognitive background questions, including the Santa Barbara Sense of Direction scale (SBSOD; Hegarty et al., 2002; Appendix B). This was completed outside of the lab.

During the experimental first session, participants entered the UCSB Brain Imaging Center waiting room and were greeted by a research assist who gave each participant an informed consent form. A head measurement was taken for EEG cap sizing. Next, blood was drawn by a trained phlebotomist in a sterile room. Participants were introduced to the navigation training maze in which they could freely move around the virtual environment in order for the RA to observe their facility with the navigation controls. Finally, the participant's feet were placed in cold water for a period of up to 90s in order to ensure that they could perform the CPT during testing sessions. If participant could not maintain submersion, they were either released or moved to a different stressor condition if possible.

During each of the next sessions, participants were met by an RA and asked to sign or initial a consent sheet. During the second session, a VO2 max measurement was taken. This process consisted of placing heart monitor electrodes on their chest and a breathing mask on their face. This mask was connected to a machine that collected information about the inspirations and expiration during a biking task in which the resistance of the pedals increased constantly until either the participants' pedal cadence dropped below a certain threshold (35 rpm) or when they surpassed or plateaued at their anaerobic threshold. This
task achieves physical exhaustion quickly and gives a measurement of aerobic capacity (i.e., a measure of physical fitness).

The third session served as a baseline session. During this session, participants were fitted with heart monitoring electrodes and the EEG cap. Next, participants salivated into a labeled cryo tube until it was full. Next, participants performed a gambling task in which they were asked to make choices between two alterative gambling choices, which presented 20 trials of differing amounts. Next, participants rested for a period of three minutes alternating between opening and closing their eyes for 90 seconds each. Next, participants completed the Operation span task (Unsworth, Heitz, Schrock, & Engle, 2005) which presented arithmetic problems and is a measure of working memory. Next, participants were introduced to three tasks they perform during the final two sessions. These tasks included a recognition memory task in which participants saw images of scenes, a visual search task, a response inhibition task, and finally retrieval of the recognition memory images. After each task, participants answered four questions relating to how averse ("How averse did you find that?"), fatiguing ("How fatiguing did you find that task?"), effortful ("How strenuous did you find that task?"), and boring ("How boring did you find that task?") they found each task. After each pressor task, participants were asked to rate their level of stress relating to that pressor. Each rating was on a scale of zero (least) to 100 (most). Participants performed a second gambling task and salivated into a cryo tube.

Figure 7 shows the sequence of events in sessions four and five, which were the session in which the navigation task was performed. In these sessions, the order of tasks and procedures was the same with the exception that during one session warm water was used (active control) while in the other session cold water was used (stress). The order of control

59

and stress conditions was counterbalanced across participants. A generalized procedure will be described for both sessions. During the fourth and fifth sessions, participants entered the testing room, initialed their consent form, were fitted with electrodes and EEG cap, gave a saliva sample, and performed the first gambling task. As in the third session, participants rested for three minutes alternating between open and closed eyes. Next, participants either encoded the recognition memory images or encoded the maze for the DSP. These two tasks were counterbalanced across participants. After this, both feet were placed in either the cold or warm water depending on the session. Participants kept their feet in the water for 90 seconds while remaining as still as possible after which they removed their feet from the water. During the next phase, participants performed the visual search task and the response inhibition task (order counterbalanced). Next participants performed another gambling task and saliva collection. During the next phase participants lowered their feet into the water again before performing either all of the navigation trials or the recognition memory retrieval trials. After each task, participants put their feet into the water to maintain their stress level. During the final phase, participants performed the final gambling task and saliva collection. As in the baseline day, after each task, participants answered four questions relating to how averse, fatiguing, strenuous/effortful, and boring they found each task on a scale of one to 100. After each water dip, participants rated their level of stress.

Figure 7. Protocol procedure across experimental stressor (cold pressor) and active control (warm pressor) testing sessions. These sessions were counterbalanced across participants.

After session 5, participants were paid for their time. After each EEG session (sessions 3-5) participants were given the option to wash their hair and provided shampoo. After all sessions were completed, the participant was debriefed on the nature of the tasks they performed.

Dual Solution Paradigm Procedure. The same general procedure for this task was used as in Experiments 1a and 1b. The differences were that approximately one hour elapsed between learning and testing, that an average of 17.67 days (*Mdn* = 7.00; *SD* = 29.91) days

elapsed between performing the task with the first maze vs the second maze, and the introduction of the stressor.

Results

The plan for this results section is to first check that the manipulation was successful in producing cortisol by comparing cortisol across session and then to compare the two conditions on each DV (solution index and efficiency).

Stress Manipulation check. Saliva samples were collected twice in the baseline session and three times across the two experimental sessions. Table 9 presents the values for cortisol across sessions and samples. Notably there is substantially elevated cortisol in the first sample of each session corresponding to entry into the lab and setup of physiological equipment and EEG electrodes. However, as can also be seen, the average amount of cortisol released between experimental sessions is greater in the stress condition than in the control (samples 2 and 3). Further, given large individual differences all samples were tested via a Kolmogorov-Smirnov test for normality. None of the samples were normally distributed, all $KS \geq 0.13$, all $p \leq 0.05$. All samples were log transformed bringing the samples into normality.

Using log transformed cortisol values as the dependent variable, a 2 (stressor condition) x 3 (cortisol samples) ANOVA indicated a significant effect of condition on cortisol, $F(1, 46) = 21.63$, $p < .001$, $\eta_p^2 = .32$, such that the cold pressor stress condition (*M* = .85, $SD = .31$) showed larger cortisol values than the warm pressor control condition ($M =$.72, *SD* = .31). Given the violation of sphericity, Greenhouse-Geisser corrections for degrees of freedom are used. There was also an effect of sample, $F(1.47, 67.41) = 41.64$, $p < .001$, η_p^2 = .48, characterized by a decreasing cortisol values from the first sample, taken at the start of the session, to the last sample taken at the end of the session. Finally, there was an

interaction, $F(2, 75.20) = 16.94$, $p < .001$, $\eta_p^2 = .27$. Simple effects analyses of cortisol sample across conditions indicated no differences between the first sample, $F(1, 45) = .29$, *p* = .59, but significant differences for both the second sample taken just after the stressor/control task, $F(1, 45) = 57.84$, $p < .001$, $\eta_p^2 = .56$, and third sample taken at the end of the session, $F(1, 45) = 7.22$, $p = .01$, $\eta_p^2 = .14$. The navigation task was temporally placed between these two cortisol samples. This analysis indicates that participants were navigating under more stress during the stress condition than the control condition.

Table 9. Aggregate level cortisol values across each condition in which saliva samples were collected. The DSP task was conducted between the second and third cortisol sample in the Stress and Control conditions. Standard deviations are presented in parentheses.

| Condition | Baseline | | | Stress (Cold Water) | | | Control (Warm Water) | |
|-----------|-----------------|----------------|---------|---------------------|--------|--------|----------------------|--------|
| Sample | | $\overline{2}$ | | $\overline{2}$ | 3 | 1 | $\overline{2}$ | 3 |
| Cortisol | 10.33 | 4.87 | 12.03 | 8.96 | 6.22 | 10.73 | 5.29 | 5.41 |
| (mmol/l) | (7.10) | (2.93) | (10.10) | (6.27) | (4.33) | (7.32) | (7.09) | (6.51) |
| Log of | | | | | | | | |
| Cortisol | 0.90 | 0.63 | 0.96 | 0.86 | 0.72 | 0.93 | 0.59 | 0.62 |
| (mmol/l) | (0.34) | (0.24) | (0.34) | (0.31) | (0.24) | (0.32) | (0.32) | (0.29) |

Subjective Task Ratings. Descriptive statistics across sessions for subjective task ratings can be found in Table 10. Participants were significantly more averse to the navigation task during the cold pressor condition. It should be noted that the range for all variable in each session was large (all *Range* \geq 70). Finally, after each water dip, participants were asked to rate their level of stress. These ratings are averaged across all dips in Table 10.

| | Control $(n = 47)$ | Stress $(n = 47)$ | t(46) | \boldsymbol{p} |
|---------------|--------------------|-------------------|-------|------------------|
| Aversion | 17.79 (22.84) | 23.04 (26.79) | 2.07 | 0.05 |
| Effort | 21.55 (19.30) | 25.91 (19.38) | 1.59 | 0.12 |
| Fatigue | 19.13 (19.58) | 21.68 (19.00) | 0.93 | 0.36 |
| Boredom | 21.23 (18.71) | 26.98 (22.97) | 1.74 | 0.09 |
| Stress | 2.93(10.61) | 67.87 (18.30) | 23.26 | ≤ 0.01 |

Table 10. Average subjective ratings after completing the Dual Solution Paradigm. Standard deviations are presented in parentheses.

Note. Some participants did not respond on all questions and were dropped from this analysis. The stress ratings were averaged over each response across foot dips. Paired samples t tests are presented.

Performance and Strategy in the DSP Navigation Trials. Successful navigation to the goal location occurred on 92.5% of all trials (across both conditions) within the 40-second time limit (Mean time $= 21.06$, $SD = 9.30$). A strict coding of the main strategies (shortcut, learned route, reversal of learned route, wandering, failure) accounted for 50.0% of all trials, while an additional 36.1% were classified by liberal coding as in Experiments 1a and 1b, leaving 13.9% uncodable. Numbers of trials coded as each strategy are shown in Table 11.

| | | Control First $(n = 25)$ | Stress First $(n = 23)$ | | |
|-----------|-------------|--------------------------|-------------------------|-------------|--|
| | Control | Stress | Stress | Control | |
| Shortcut | 8.28 (3.81) | 9.36(3.55) | 7.96(4.71) | 8.43 (4.88) | |
| Learned | 4.24(3.24) | 3.88(3.18) | 5.87(5.59) | 5.26(5.57) | |
| Reversal | 2.48(1.58) | 1.84(1.37) | 1.61(1.41) | 1.57(1.31) | |
| Wandering | 0.44(0.77) | 0.64(0.91) | 0.61(0.89) | 0.39(0.72) | |
| Uncodable | 2.80(1.96) | 3.00(1.87) | 2.57(1.70) | 2.74(2.09) | |

Table 11. Average number of trials out of 20 coded as each route selection by condition across order in which the two conditions were completed. Standard deviations are presented in parentheses.

In terms of individual differences, across both sessions and conditions, participants showed a wide range of strategy preference from nearly all non-shortcut routes to nearly all shortcuts (Control First order: Session 1 Range of $SI = .06$ to .85; Session 2 Range of $SI =$.05 to 0.90) as in Experiments 1a and 1b and previous research on this task. The same was true for the second order (Stress First order: Session 1 Range of SI = .00 to .78, Session 2 Range of $SI = .05$ to $.95$). As can be seen in Figure 8, there was a strong positive correlation between SI in the stress and control conditions, $r(46) = .72$, $p < .001$, indicating participants typically used the same strategy in the two condition, regardless of order.

Figure 8. Scatterplot of the Solution Index measure from both control and stress conditions indicating high similarity of strategy behavior across conditions.

Effect of Stress on Navigation Performance. Using a 2 (stressor condition) x 2 (order) ANOVA using number of successful trials out of 20 as the dependent variable, there was no main effect of condition, $F(1,46) = 2.08$, $p = 0.15$. There was no main effect of order, $F(1,46)$ $= .000, p = 1.00$. Finally, the interaction between condition and order was not significant, $F(1, 46) = 0.35$, $p = 0.56$. This is not surprising as performance was generally high across all navigators.

It is possible that stress only influenced success of navigation the outset of each set of navigation trials. Therefore, an analysis was conducted across each set of ten trials. Using a 2 (stressor condition) x 2 (set: first ten trials vs second ten trials) x 2 (order) ANOVA was conducted on number of successful trials. There were no main effects nor interactions, all $F(1, 46) \le 2.62$, all $p \ge 11$. These analyses indicated that participants were navigating as effectively in the cold pressor (stress) condition as in the warm water (control) condition.

Effect of Stress on Navigation Strategy in the DSP. A 2 (stressor condition) x 2 (order) ANOVA with solution index as the dependent variable indicated no main effect of condition, $F(1, 46) = .13$, $p = .72$, nor a main effect of order, $F(1, 46) = .29$, $p = .59$. However, there was a trending interaction between condition and order, $F(1, 46) = 3.57$, $p =$.07, $\eta_p^2 = 0.07$. As seen in Table 12, participants were more likely to take a shortcut on the second task they performed, but the gain from session 1 to 2 was larger when the control session was first.

Further, Figure 9 shows change in strategy between sessions across order type. The light gray circle represents solution index during the control session while the dark gray triangle represents strategy during the stressor session. Their descending organization is based on the performance of the first task completed. The line connecting them represents the amount of change across sessions. Generally, this type of plot shows amount of movement in strategy shift from session to session. Here, Figure 9 indicates that participants take more shortcuts in the second session, regardless of whether it is the control or the stress condition.

Figure 9. Dumbbell plots showing solution index values for each condition across order. Light gray circles represent solution index during the control session (warm water) and dark gray triangles represent solution index during the stress (cold water).

In these navigation trials, participants sometimes change routes within a trial and walk on steps they have already traversed. This is known as retracing. One hypothesis is that participants retrace more routes in the stressor condition due to directional confusions. However, a 2 (condition) x 2 (order) ANOVA using the number of retrace trials as the dependent variable revealed no main effects or interaction were found, all $F(1, 46) \le .50$, all $p \geq 0.49$, indicated no evidence for more retracing due to stress.

Finally, it is possible that stress was more harmful in the expression of their strategy during the first half of trials rather than the last half. In a 2 (stressor condition) x 2 (set: first vs second half of trials) x 2 (order) ANOVA on the number of shortcut trials, there were no main effects of condition, $F(1, 46) = .55$, $p = .46$, nor order, $F(1, 46) = .32$, $p = .58$. However, there was a main effect of set, $F(1, 46) = 6.64$, $p = .01$, $\eta_p^2 = .13$, such that more shortcuts were taken in the second half ($M = 4.57$, $SD = 2.58$) than the first half ($M = 3.95$, *SD* = 2.21) of trials in each session. There was a trending interaction between condition and condition order, $F(1, 46) = 3.40$, $p = .07$, $\eta_p^2 = .07$, such that participants took more shortcuts in the stress condition, contrary to the prediction. However, no other interactions were found, all $F(1, 46) \le 2.51$, all $p \ge .12$.

| | Control First $(n = 25)$ | | Stress First $(n = 23)$ | | |
|-----------------|--------------------------|---------------|-------------------------|--------------|--|
| | Control | Stress | Stress | Control | |
| Success | 18.24(1.81) | 18.76 (1.59) | 18.61(1.80) | 18.39(1.50) | |
| Solution Index | 0.45(0.19) | 0.50(0.17) | 0.42(0.24) | 0.46(0.25) | |
| Time | 20.88 (4.63) | 20.69(4.15) | 21.33(4.01) | 21.41 (4.24) | |
| Path Efficiency | 2.20(0.45) | 2.24(0.53) | 2.35(0.44) | 2.30(0.48) | |

Table 12. Descriptive statistics of each objective measure across order in which the two conditions were completed. Standard deviations are presented in parentheses.

Note. Success is out of 20.

Effect of Stress on Efficiency in the DSP Navigation Trials. Using a 2 (stressor condition) x 2 (order) ANOVA using *time* efficiency as the dependent variable, there was no a main effect of condition, $F(1, 46) = .09$, $p = .77$, nor order, $F(1, 46) = .26$, $p = .62$. There was no interactions, $F(1, 46) = .01$, $p = .90$. Finally, a 2 (stressor condition) x 2 (order) ANOVA using path efficiency data as the dependent variable indicated no main effects of

condition, $F(1, 46) = .44$, $p = .51$, order, $F(1, 46) = .75$, $p = .39$, nor an interaction, $F(1, 46)$ $= .01, p = .93.$

Initial movement and dwell measures. The descriptive statistics for each measure of dwell can be found in Table 13. One possibility is that people take longer to start moving on each trial when under stress. Average time to first movement across trials was used as the dependent variable in a 2 (stressor condition) by 2 (order) ANOVA. No differences were found between conditions, $F(1, 46) = 1.03$, $p = .32$, nor orders, $F(1, 46) = .002$, $p = .97$. Further there was no interaction, $F(1, 46) = .01$, $p = .93$. Another possibility is that participants struggle to navigate through the environment and stop more across trials. Participants average total dwell count across trials and average number stops equal to or longer than .5s across trials were evaluated using a 2 (stressor condition) x 2 (order) ANOVA. No main effects nor interactions were found, all $F(1, 46) \le 1.19$, all $p \ge 2.28$.

Correlations of Performance Measures with Self-Report Measures. There were no significant correlations between the SBSOD and the navigation task variables (two variables had significant correlations but did not survive when removing one extreme outlier). In terms of the subjective task ratings and SBSOD, participants with lower SOD tended to be more

averse to the navigation task in the stress condition, $r(45) = -0.28$, $p = 0.06$, found the task significantly more effortful in both the stress condition, $r(45) = -.30$, $p = .04$, and the control session, $r(45) = -.37$, $p = .01$, and found the navigation task significantly more fatiguing in both the stress, $r(45) = -.40$, $p = .006$, and control conditions, $r(45) = -.39$, $p = .006$.

Many correlations between the subjective ratings and the navigation task variables were significant between the subjective ratings and the navigation task variables. Participants with lower SI (less shortcuts) in the stress condition rated themselves as more averse to the task, $r(45) = -.31$, $p = .04$, found it more fatiguing, $r(45) = -.30$, $p = .04$. In general, participants who found the navigation task more effortful they found the task during the stress condition took longer per trial, $r(45) = .30$, $p = .04$, were more averse to the task, $r(45)$ $= .36$, $p = .01$, and were more likely to be bored, $r(45) = .30$, $p = .04$. Similar results were found for path efficiency per trial, all $r(45) \ge .27$, all $p \le .06$, except boredom. Specifically, the more averse a participant was to the task during the stress condition, the lower their path efficiency, $r(45) = .41$, $p = .005$.

Analysis of individual differences in cortisol and navigation. As noted above, there were large individual differences in cortisol expression within condition. This is a wellknown effect in the literature (Buchanan et al., 2006; Lupien et al., 2007). Therefore, the analyses above mixes people that respond to the stress and those that do not. In the following analyses, participants were grouped by their log transformed cortisol reaction via a regression of their stress condition day stress on their control day cortisol values. Residuals from this analysis were computed such that positive values indicated more cortisol reaction to the stressor than the control condition. A median split was performed on the residuals (*Mdn* = .01). Twenty four participants were categorized as high responders and 24 were categorized as low responders.

Participants in the high and low cortisol split did not differ in terms of self-reported sense of direction, $t(45) = 1.41$, $p = .17$. A 2 (condition) by residual median split (high vs low) repeated measures ANOVA was conducted on each measure of interest in the DSP presented above (performance, solution index, and efficiency measures). No main effects nor interactions were significant, all $F(1, 46) \le 2.53$, all $p \ge 0.12$.

Discussion

The cold pressor task was successful in elevating cortisol levels more in the stress condition than in the control condition. The amount of cortisol elicited to the cold pressor is consistent with the previous literature (see Table 1). Further, the effects of the stressor were also readily apparent in the subjective ratings of stress generated during the cold pressor and warm water tasks. There participants indicated very stressful reaction to the cold water over the warm water task.

The results from the navigation task, however, indicated that navigation strategy and

efficiency are robust to this type of stressor. Participants were not more inclined to navigate via learned routes in the stressor, ice water, condition relative to the control, warm water, condition. Instead, what is seen is a practice effect (Boone et al., 2019) such that participants are more likely to take shortcuts in the second session, regardless of stress condition.

A more direct, albeit post-hoc, comparison between participants with high and low levels of stress response did not show differences between the stress and control conditions any of the measures of performance, strategy, or efficiency of navigation. Overall, these results suggests that the cold pressor task has little influence over navigation performance, strategy, or efficiency.

Experiment 3: Trier Social Stressor Task and Navigation Strategy and Efficiency

Whereas the cold pressor task represents a physiological threat to the human body, social-evaluative stressors have shown to be a more reliable method in which to increase cortisol relative to baseline measures (Dickerson & Kemeny, 2004). These stressors consist of asking the participants to perform a task that can be evaluated in a social context such as public speaking or performing arithmetic in front of peers. The premier task to carry out such a stressor is the Trier Social Stress Task in which participants are suddenly asked to perform a speech on why they would be an ideal candidate for their dream job in front of a panel of peers and are then asked to perform a mental arithmetic task of subtracting from 1022 by 13 (Kirschbaum et al., 1993). This task has shown four-fold increases of cortisol release relative to baseline (Kemeny & Dickerson, 2004). Further, other work has indicated hippocampal deactivation during stress of this type of social stressor (Pruessner et al., 2008; Oei et al., 2007). Other work has indicated that the social-evaluative component of the Trier Social Stressor is what drives the stress response rather than the presence of others per se. Nonevaluative, and/or "friendly" versions of the task without the negative aspects of the panel of judges does not show the same increase relative to baseline cortisol (Dickerson, Mycek, & Zaldivar, 2008; Het, Rohleder, Schoofs, & Wolf, 2009; Wiemer, Shoofs, & Wolf, 2013).

The social evaluative stressor class offers an interesting comparison condition to that of physiological threat in that it is not about physical relationships to the surrounding world or the task itself. Rather, the stress response arises from the social evaluation of those in the situations. There are parallels to when something like this may happen in a navigation context. For instance, social stress in a navigation context might become salient when driving friends to a meeting downtown. One may take a wrong turn as threat of social evaluation

75

builds up, leading to potentially getting lost. In this way, social stressors may disambiguate from physiological stressors.

Two studies have investigated navigation processes relating to the Trier Social Stressor task. In each study, participants were asked to learn some environmental layout before being tested on their knowledge of that layout. Thomas et al. (2010) presented participants with a task similar to a virtual Morris water maze in which participants learned the location of visible targets. During retrieval trials, participants were asked to move towards these now invisible targets. They found that only females in the stressor condition were hindered by the social stressor task of giving a speech. Klopp et al. (2012) also used the Trier social stress task of giving a speech and then ask participants perform a virtual Morris water maze task. No differences were found between the stressor or control group in this task. However, both studies applied the stressor before learning. In contrast, Experiment 3 applied the social stressor between testing and learning to directly evaluate the effects of stress on retrieval.

During Experiment 3 navigation strategy was measured twice. During one session, participants navigated in the DSP trials after performing the full Trier protocol. During a second session on another day participants navigated in the DSP after a modified active control version of Trier in which they gave a speech concerning their daily routine in a room with an inattentive researcher. As in Experiment 3, it is predicted that, if place navigation is disrupted by stress due to increased levels of cortisol, then participants should take fewer shortcuts in the stressor condition than in the control condition. Alternatively, the effect of stress could also be seen in measures of efficiency such that participants should take more time and show less path efficiency when under social stress than in the control condition.

76

Methods

Participants

Participants were 40 University of California, Santa Barbara students (20 females) participating for 20 dollars per hour of their time. One female participant was dropped due to motion sickness related issues. There was no difference between condition order on SBSOD, $t(37) = 1.33, p = .19.$

Design

A 2 (stressor condition: Stressor vs Active Control) x (order: Control – Stressor vs Stressor-Control) design was used. Session and maze type were manipulated within subjects and order of sessions was counterbalanced. Order of conditions was manipulated between subjects.

Materials and Apparatus

All materials used in Experiment 3 are used here with the exception that the cold pressor task (CPT) was replaced with the Trier Social Stress Test (TSST) as the stressor. An 8 foot tall x 10 foot long room divider was used to create a speech preparation room section and a panelist section in a large room (30 by 30 feet). The divider was affixed with Helvetica boldfaced letters (font size 144) from A to G arranged in a grid for eye tracking calibration. Panelists used a stopwatch to record speech timing. A Pupil Labs mobile eyetracker (Berlin, Germany) was used to record eye movements as well as real world audio and video during the Trier task.

Procedure

The procedure for Experiment 3 is similar to Experiment 2. All general procedures were the same regarding sessions 1-3 including procedures regarding physio electrode

placement and EEG capping.

Sessions 4 and 5 differed from Experiment 2 in the following ways. During sessions 4 and 5, the participant entered the lab and initialed their consent form and physio electrodes and EEG cap were placed. Participants gave a saliva sample and performed the gambling task. Next, participants learned either the recognition memory image set or the navigation maze. These tasks were counterbalanced. Next, participants were moved by the RA to a large room set up with the room divider. Once all electronic equipment was turned on and recording, participants were read information regarding the task they were about to perform depending on the condition. For the stressor condition, after a short baseline period, participants were told they would be given ten minutes to prepare a five-minute speech on why they would be the ideal candidate for their dream job. They were told they would be recorded on video and audio. They were allowed to ask questions and time started. After ten minutes, the room divider was removed revealing three female peer-aged panelists. Then, the participant was told they were to deliver their speech to the panelists for five minutes. If the participant stopped speaking for 20s consecutively they were instructed to continue. After the five-minute speaking task, they were told they would complete a math task in which they must subtract 1022 by 13 (as in the traditional Trier task). If they were incorrect, they were directed to start over from 1022.

For the active control condition, participants were given a similar set of instructions except that the speech was to be about their everyday routine in order to avoid emotionally evocative talking points (Het et al., 2009; Dickerson et al., 2008). Further, they gave their speech to the room divider and one RA was in the room but not paying attention to their speech. This RA served as a check to make sure they spoke for the entire time and advanced

78

the procedure. Next participants completed simple addition task. They were asked to start at zero and mentally add by fives. Finally, in both conditions, after all Trier components were completed, participants were asked to rest for five minutes and were moved back to the testing room.

During the testing portion, the navigation task was counterbalanced across condition order with the recognition memory task. See Figure 10 for a description of order of tasks. The same DSP procedure was used as in Experiments 1a, 1b, and 2.

Dual Solution Paradigm Procedure. The same general procedure for the Dual Solution Paradigm was used as in Experiment 2. Approximately one hour elapsed between learning and testing and an average of 15.53 days (*Mdn* = 7.00; *SD* = 20.96) days elapsed between performing the task with the first maze versus the second maze.

Results

The plan for this results section is to check that the manipulation was successful in producing cortisol by comparing cortisol across session and then to compare the two conditions on each DV (solution index and efficiency).

Stress Manipulation check. As in Experiment 2, saliva samples were collected twice in the baseline session but four times across the two experimental condition sessions. Table 15 presents the values for cortisol across sessions and samples. Cortisol sample 2 was just before the stressor/control task was applied. Cortisol sample 3 was about ten minutes after the stressor was applied. Cortisol sample 4 was taken at the end of each experimental session. In the raw cortisol values, it is notably that there is substantially elevated cortisol in the first sample of each session (relative to other samples) corresponding to entry into the lab and setup of physiological equipment and EEG electrodes. While there was a reduction in cortisol at the second sample in both conditions, there is also a large peak for the third sample linked to the speech task. Given individual differences in cortisol elicitation, all samples were tested via a Kolmogorov-Smirnov test for normality. Only the control sample 3 was normally distributed, $KS = .13$, $p = .11$, all other samples *were not* normally distributed, all $KS \ge .14$, all $p \leq 0.04$. All samples were log transformed, bringing all but the final sample in the control condition to normality, $KS = .15$, $p = .03$.

The first sample of each sample was eliminated in order to test the reaction to the stressor itself. Using log transformed cortisol values as the dependent variable, a 2 (condition: stress vs control) x 3 (cortisol samples: sample 2, sample 3, sample 4) ANOVA indicated a significant effect of condition, $F(1, 38) = 5.01$, $p = .03$, $\eta_p^2 = .12$, such that the stress condition ($M = .80$, $SD = .23$) showed larger cortisol values than the control group (M

80

= .75, *SD* = .25). Given the violation of sphericity, Greenhouse-Geisser corrections for degrees of freedom are used. There was a significant effect of sample, $F(1.82, 69.06) =$ 22.62, $p < .001$, $\eta_p^2 = .37$, characterized by a peak in cortisol values in the third (post-stress) sample compared to the second sample and fourth sample. Finally, the interaction was significant, $F(1.54, 58.51) = 5.30$, $p = .01$, $\eta_p^2 = .12$. Simple effects analyses of sample across conditions indicated no differences between conditions on the second (pre-stressor) sample, $F(1, 38) = .41$, $p = .74$. A significant difference was found between the conditions on the third (post-stressor) sample, $F(1, 38) = 9.59$, $p = .004$, $\eta_p^2 = .20$, but was marginal for the fourth (final) sample, $F(1, 38) = 4.16$, $p = .05$, $\eta_p^2 = .10$. This analysis indicates that participants were navigating under more stress during the stress condition than the control condition.

Subjective Task Ratings. As in Experiment 2, after the navigation task, participants gave responses to four questions on a 0 to 100 point scale (aversion, effort, fatigue, and boredom) pertaining to the navigation task itself, and a final stress rating relating to the stress of the stress/control condition. Descriptive statistics across conditions can be found in Table 16. It should be noted that the range for all variable in each session was large (all *Range* \geq 70). No differences were found between any these measures relating to their feelings about the navigation task. Finally, there was a significant difference between ratings for the stressor and control conditions.

Table 15. Aggregate level cortisol values across each condition in which saliva samples were collected. The DSP task was conducted between the third and fourth cortisol sample in the Stress and Control condition. Standard deviations are presented in Table 15. Aggregate level cortisol values across each condition in which saliva samples were collected. The DSP task was
conducted between the third and fourth cortisol sample in the Stress and Control condition. Standard

| | Control $(n = 33)$ | Stress $(n = 33)$ | t(32) | \boldsymbol{p} |
|---------------|--------------------|-------------------|-------|------------------|
| Aversion | 32.27 (32.51) | 37.45 (29.08) | 1.18 | 0.25 |
| Effort | 29.09 (26.55) | 30.97 (21.72) | 0.56 | 0.58 |
| Fatigue | 33.16 (27.00) | 31.75 (23.81) | 0.29 | 0.77 |
| Boredom | 36.58 (29.39) | 35.00 (22.91) | 0.36 | 0.72 |
| Stress | 27.18 (21.82) | 61.68(26.13) | 9.03 | $\leq .001$ |

Table 16. Average subjective ratings after completing the Dual Solution Paradigm. Standard deviations are presented in parentheses.

Note. Some participants did not make ratings due to computer error. Paired samples t tests are presented.

Performance and Strategy in the DSP Navigation Trials. Successful navigation to the goal location occurred on 88.9% of all trials (across both the stress and control conditions) within the 40-second time limit (*Mean time* = 22.74, *SD* = 9.57). Descriptive statistics for each category can be found in Table 17. A strict coding of the main strategies (shortcut, learned route, reversal of learned route, wandering, failure) accounted for 48.8% of all trials, while 37.8% of the trials were coded as liberal and the rest (13.4%) were uncodable.

Table 17. Average number of trials out of 20 coded as each route selection coding by condition across order in which the two conditions were completed. Standard deviations are presented in parentheses.

| | Control First $(n = 18)$ | | Stress First $(n = 21)$ | | |
|-----------|--------------------------|---------------|-------------------------|------------|--|
| | Control | Stress | Stress | Control | |
| Shortcut | 5.72(4.50) | 7.28(3.85) | 6.05(4.20) | 7.62(4.23) | |
| Learned | 6.11(5.40) | 5.22(4.63) | 6.67(4.37) | 4.76(3.73) | |
| Reversal | 2.50(1.95) | 2.33(1.65) | 2.38(1.99) | 2.19(1.78) | |
| Wandering | 0.72(1.18) | 0.22(0.43) | 0.33(0.58) | 0.29(0.46) | |
| Uncodable | 2.44(1.89) | 2.44(1.89) | 2.86(1.77) | 2.90(1.97) | |

In terms of individual differences, as seen in Figure 11, across both sessions and conditions, participants showed a wide range of strategy preference from nearly all nonshortcut routes to nearly shortcuts (Control First order: Session 1 Range of SI = .00 to .95, Session 2 Range of $SI = .05$ to $.85$) as in Experiment 1 and previous research on this task. The same was true for the second order (Stress First order: Session 1 Range of SI = .05 to .75, Session 2 Range of $SI = .05$ to .85). Importantly, there was a strong positive correlation in solution index between the two conditions, $r(21) = .82$, $p < .001$, indicating that participants typically used the same strategy in the stress and control conditions.

Figure 11. Scatterplot of the Solution Index measure from both sessions indicating high similarity of strategy behavior across sessions and order in the Trier Social Stress Test condition.

Effect of Stress on Performance in the DSP Navigation Trials. As seen in Table 18,

there was little difference in success rates between the stress and control condition. A 2

(stressor condition) x 2 (order) ANOVA using number of successful trials as the dependent variable indicated was no main effect of stressor in terms of success, $F(1, 37) = .72$, $p = .41$. There was no main effect of order, $F(1, 37) = .88$, $p = .40$. Finally, there was no interaction between stress condition and order, $F(1, 37) = .72$, $p = .41$. It is possible that stress only influenced the outset of each set of navigation trials. Therefore, an analysis was conducted across the first and second set of ten trials. Using a 2 (stressor condition) x 2 (set: first ten trials vs second ten trials) x 2 (order) ANOVA was conducted on number of successful trials. There was as main effect of set, $F(1, 37) = 7.95$, $p = .008$, $\eta_p^2 = .18$, such that more trials were successfully completed in the second set ($M = 9.06$, $SD = 1.15$) than the first set ($M =$ 8.70, *SD* = 1.21). There were no other significant main effects or interactions, all $F(1, 37) \le$ 1.85, all $p \ge 18$. These analyses indicate that participants were navigating as effectively in the job speech (stressor) condition as in the control daily routine speech session.

Effect of Stress on Strategy in the DSP Navigation Trials. Table 18 presents descriptive statistics for each measure of strategy and efficiency. A 2 (stressor condition) x 2 (order) ANOVA using solution index as the dependent variable indicated no main effect of condition, $F(1, 37) = .01$, $p = .92$, nor a main effect of order, $F(1, 37) = .01$, $p = .92$. However, there was a significant interaction of condition by order, $F(1, 37) = 14.49$, $p =$.001, η_p^2 = .28, which represents a general practice effect, such that the second session in each order showed more shortcutting, as seen in Table 17. Most notably, as can be seen in Figure 12 most participants take more shortcuts in their second session regardless of condition. The light gray circle represents solution index during the control session while the dark gray triangle represents strategy during the stressor session. Their descending order of participants is based on performance in the first task completed. The line connecting them

represents the amount of change across session. The major indication from this plot is that participants take more shortcuts in the second session, regardless of whether it is the control or the stress condition.

Figure 12. Dumbbell plot showing solution index values for each condition across order. Light gray circles represent solution index during the control session (daily routine speech) and dark gray triangles represent solution index during the stress (ideal job speech).

Further, in these navigation trials, participants sometimes change routes within a trial and walk on steps they have already traversed, retracing their route. It is possible that stress leads to more retracing through directional confusions. Using a 2 (condition) by 2 (order)

ANOVA on retracting count data indicated no significant main effects nor an interaction, all *F*(1, 37) ≤ 2.51, all p ≥ .12.

Finally, it is possible that stress was more harmful during the first half of trials rather than the last half. In a 2 (stressor condition) x 2 (set: first vs second half of trials) x 2 (order) ANOVA using shortcut count as the dependent variable. There were no main effects of stress on conditions, $F(1, 37) = .000$, $p = .99$, nor order of condition, $F(1, 37) = .07$, $p = .80$. However, there was a main effect of set, $F(1, 37) = 7.22$, $p = .01$, $\eta_p^2 = .16$, such that more shortcuts were taken in the second half ($M = 3.59$, $SD = 2.37$) than the first half of trials ($M =$ 3.08, *SD* = 2.26). There was a significant interaction between condition and condition order, $F(1, 37) = 12.45$, $p = .001$, $\eta_p^2 = .25$, which reflects a practice effect. However, no other interactions were found, all $F(1, 37) \le .50$, all $p \ge .49$.

Effect of Stress on Efficiency in the DSP Navigation Trials. A 2 (stressor condition) x 2 (order) ANOVA using *time* efficiency data as the dependent variable, there was no main effect of condition, $F(1, 37) = .72$, $p = .40$, nor order, $F(1, 37) = .97$, $p = .33$. There was no interaction between stress condition and order, $F(1, 37) = .17$, $p = .68$. Finally, a 2 (stressor condition) x 2 (order) ANOVA using path efficiency data as the dependent variable indicated no main effects of condition, $F(1, 37) = .65$, $p = .43$, or order, $F(1, 46) = .29$, $p = .59$, nor an interaction of these factors, $F(1, 46) = .93$, $p = .34$.

| | Control First ($n = 18$) | | | Stress First $(n = 21)$ |
|-----------------|----------------------------|---------------|---------------|-------------------------|
| | Control | Stress | Stress | Control |
| Success | 17.50(1.98) | 17.50(2.09) | 18.29 (1.74) | 17.76(2.14) |
| Solution Index | 0.32(0.23) | 0.41(0.19) | 0.33(0.21) | 0.42(0.21) |
| Time | 23.74 (4.62) | 23.11 (4.14) | 22.06(4.11) | 22.27(4.30) |
| Path Efficiency | 2.50(0.47) | 2.38(0.44) | 2.37(0.41) | 2.36(0.46) |

Table 18. Descriptive statistics of each objective measure across order in which the two conditions were completed. Standard deviations are presented in parentheses.

Initial movement and dwell measures. One possibility is that people take longer to start moving on each trial when under stress. Descriptive measures for each variable can be found in Table 19. Average time to first movement across trials was used as the dependent variable in a 2 (stressor condition) by 2 (order) ANOVA. No differences were found between conditions, $F(1, 37) = .02$, $p = .90$, order, $F(1, 37) = .15$, $p = .70$. Further there was no interaction of these factors, $F(1, 37) = 2.54$, $p = .12$. Another possibility is that participants struggle to navigate through the environment and stop more across trials. Participants average total dwell time across trials and average number stops equal to or longer than .5s across trials were evaluated using a 2 (stressor condition) x 2 (order) ANOVA. No main effects nor interactions were found, all $F(1, 37) \le 1.13$, all $p \ge .29$, indicating that participant did not dwell more in the stress condition relatively to the control condition.

| | Control First $(n = 18)$ | | Stress First $(n = 21)$ | | |
|---------------------|--------------------------|---------------|-------------------------|------------|--|
| | Control | Stress | Stress | Control | |
| Initial Movement | 1.72(0.68) | 1.60(0.57) | 1.78(0.57) | 1.68(0.66) | |
| Dwell Counts | 1.11(0.81) | 0.99(0.97) | 0.86(0.71) | 0.77(0.59) | |
| Half Second Stops | 0.45(0.40) | 0.43(0.40) | 0.40(0.49) | 0.33(0.34) | |

Table 19. Descriptive statistics of each measure of dwelling across order in which the two conditions were completed. Standard deviations are presented in parentheses.

Correlations of Performance Measures with Self-Report Measures. SBSOD was correlated significantly with success during the stress condition, $r(39) = .40$, $p = .01$, indicating that higher SOD scores were associated with better performance on the DSP. In terms of the subjective task ratings and SBSOD, participants with lower SOD were more fatigued by the navigation task in the stress condition, $r(45) = -.37$, $p = .03$, and found the task significantly more effortful, $r(45) = -.34$, $p = .04$.

There was a negative relationship between success during the stress condition and boredom ratings, $r(39) = -.36$, $p = .03$. In general, ratings indicated that the more boring the task was, the longer it took to solve during the stress condition, $r(39) = -.33$, $p = .05$, and the further participants travelled, $r(39) = -.44$, $p = .01$.

Analysis of individual differences in cortisol and navigation. As noted above, there were large individual differences in cortisol expression within condition. In the following analyses, participants were grouped by their log transformed cortisol reaction via a regression of their cortisol on the stress condition day on their control day cortisol values. Residuals from this analysis indicated that positive values indicated more reaction to the stressor than the control stressor. A median split was performed on the residuals (*Mdn* = 0.03). Nineteen

participants were categorized as high responders and 20 were categorized as low responders. A 2 (condition) by residual median split (high vs low) repeated measures ANOVA was conducted on each measure of interest in the DSP. No main effects nor interactions were significant, all $F(1, 37) \le 2.97$, all $p \ge .09$.

Discussion

The Trier social stressor task in this experiment was successful in elevating cortisol levels in the stress compared to the control condition. This is similar to the results of the subjective ratings of stress after each stressor conditions indicating large differences in how stressful the participants felt the task was overall. However, the amount of cortisol elicited by the TSST is a bit lower than would be excepted from the literature (see Table 1) and the result that the control condition also elevated cortisol relative to baseline inconsistent with the literature (Het et al., 2009; Weimers et al., 2013; Dickerson et al., 2008). Altogether, this suggest that the TSST did stress our participants although not as clearly as indicated by the vast literature on this task.

The lack of a large difference between the stressor conditions clarifies the results in terms of the navigation task. In general, the results showed that navigation strategy and efficiency were largely unchanged between the conditions. Participants were not more inclined to navigate via learned routes in either condition. As in Experiment 2 and previous work on using the Dual Solution Paradigm, there was a sizeable practice effect (Boone et al., 2019) such that participants were more likely to take shortcuts in the second session, regardless of stress condition. Post-hoc comparisons of high and low cortisol responders did not indicate the predicted changes in navigation performance, strategy, or efficiency.

Table 20. Correlation table for each measure of the Dual Solution Paradigm across the stress (first row) and control (first column)

Table 20. Correlation table for each measure of the Dual Solution Paradigm across the stress (first row) and control (first column)

Experiment 4: Cognitive Fatigue Task and Navigation Strategy and Efficiency

One stressor type that has been seen little study in the stress and cognitive literature is cognitive fatigue and frustration. In one isolated study that used this type of stressor and examined a spatial task, Richardson and VanderKaay Tomasulo (2012) used the mirror star tracing task to induce a stress response. The found little effect of this stressor on spatial tasks such as pointing judgments in a learned environment. However, this may have been due to the relative low levels of cortisol associated with the stressor, in general.

Another task meant to induce a stress response that is similar to a frustration task is scheduling. The scheduling task was developed as a means for studying strategy development in problem solving (Taatgen, 1999). The literature on this task as it relates to stress is non-existent. However, protocol analysis of participants performing this task indicates frustration with the more complex problems as working memory is overloaded (see Taatgen, 1999). Therefore, this set of tasks would simulate situations under which people could be cognitively fatigued and/or frustrated. This stressor is more akin to vigilance in the field which can be stressful but differs from that of psychological and physiological threat. However, it remains to be seen whether a stress response via cortisol would arise in this task or whether some other processes may cause detriments to navigation strategy. Thus, this experiment can be compared with the other stressors to understand what, if any, effect it may have on navigation strategy usage.

During Experiment 4 navigation strategy was measured twice. In the stress condition, participants navigated in the DSP trials after performing the full cognitive fatigue protocol. On another day participants navigated in the DSP after an active control version of the task in which they perform a simple word search task. As in Experiments 2 and 3, it is predicted that

participants will take fewer shortcuts and be less efficient in the cognitive fatigue (scheduling) condition relative to the control conditions.

Methods

Participants

Participants consisted of 40 University of California, Santa Barbara students (20 females) participating for 20 dollars per hour of their time. Two female participants were excluded (motion sickness or quit early). Note that there was a difference between condition orders on SBSOD, $t(36) = 2.22$, $p = .03$, $d = .72$, such that those in the Control-Stress order rated themselves as having a significantly better sense of direction $(M = 4.51, SD = 1.15)$ than those in the Stress-Control order $(M = 3.77, SD = .88)$.

Design

A 2 (stressor condition: Stressor vs Active Control) x (order: Control – Stressor vs Stressor-Control) design was used. Session and maze type were manipulated within subjects and order of sessions was counterbalanced. Order of conditions was manipulated between subjects.

Materials and Apparatus

All materials used in Experiment 2 used here with the exception of CPT related materials. A Pupil Labs mobile eyetracker (Berlin, Germany) was used to record eye movements as well as real world audio and video during all tasks.

Procedure

The procedure for Experiment 4 is similar to Experiment 2 with some exceptions. First, all general procedures were the same regarding sessions 1-3 and procedures regarding physio electrode placement and EEG capping.

During sessions 4 and 5 (Figure 13), the participant entered the lab and initialed their consent form and physio electrodes and EEG cap were placed. Participants gave a saliva sample and performed the gambling task. The order of tasks and procedures were the same with the exception that during one session participants completed the scheduling task (stress) while in the other session they completed the word search task (active control). As in the third session, participants rested for three minutes alternating between open and closed eyes. Next, participants either encoded the recognition memory images or encoded the maze for the DSP. These two tasks were counterbalanced across participants.

Figure 13. Protocol procedure across experimental stressor (cognitive fatigue task) and active control (word search task) testing conditions. These conditions were counterbalanced across participants.

During the next phase, participants completed either the scheduling task or the word search task. The scheduling task was adapted from Taatgen (1999) in which participants act as a manager that must schedule employee tasks. Participants are given several parameters in order to solve a trial such as the number of works, the amount of time each task took, and the order in which the tasks must be completed. Difficulty of the trials increases across the trials by including additional workers, number of tasks, and task order constraints. See Figure 14a
for a visual representation. Two practice trials were given and nineteen total test trials were included. Trials had rewards depending on solve time. Each trial had a time limit of 10-12 minutes and rewards decreased by fifty cents per each minute used. If all trials were completed within the two hours, the same set was re-started. No aids were allowed. In contrast, the control task included a word search. Participants were asked if a particular word was present or absent amongst a matrix of distractor words (30 rows x 5 columns). Rewards were given for correct answers. There were no time limits per word. See Figure 14b for a visual representation.

Figure 14. Images from the stressor scheduling task (a) and control word search task (b).

After completing the stress task or control task, participants performed another gambling task and saliva collection. After this, participants performed each of four tasks: the visual search task, the response inhibition task, the recognition memory task, and the navigation task (order counterbalanced). Note that the same DSP procedure was used as in Experiments 1a, 1b, 2, and 3. This was followed by a collection of saliva.

After each EEG session (sessions 3-5) participants were given the option to wash their hair and provided shampoo. After all sessions were completed, the participant was debriefed on the nature of the tasks they performed. After session 5, participants were paid for their time.

Dual Solution Paradigm Procedure. The same general procedure for this task was used as in Experiment 2. Approximately one hour elapsed between learning and testing and an average of 32.32 days (*Mdn* = 24.50; *SD* = 24.09) days elapsed between performing the task with the first maze vs the second maze.

Results

The plan for this results section is to check that the manipulation was successful in producing cortisol by comparing cortisol across session and then to compare the two conditions on each DV (solution index and efficiency).

Stress Manipulation check. Saliva samples were collected twice in the baseline session and three times across the two experimental sessions. Table 21 presents the values for cortisol across sessions and samples. Cortisol sample 1 was taken after the EEG and physio recording preparations. Cortisol sample 2 was just after the stressor was applied while cortisol sample 3 was taken at the end of each experimental session. In the raw cortisol values, there is substantially elevated cortisol in the first sample of each session

corresponding to entry into the lab and setup of physiological equipment and EEG electrodes. All samples were tested via a Kolmogorov-Smirnov test for normality. The samples in the stressor condition were normally distributed, all $KS \leq .14$, all $p \geq .06$, while the control conditions samples were not normally distributed, all $KS \geq .20$, all $p \leq .001$. All samples were log transformed, bringing the samples into normality.

Table 21. Aggregate level cortisol values across each condition in which saliva samples were collected. The DSP task was conducted between the second and third cortisol sample in the Stress and Control conditions. Standard deviations are presented in parentheses.

| | | | | Stress | | | Control | |
|-----------|-----------------|----------------|--------|-------------------|--------|--------|----------------|--------|
| Condition | Baseline | | | (Scheduling Task) | | | (Word Search) | |
| Sample | | $\overline{2}$ | | $\overline{2}$ | 3 | | $\overline{2}$ | 3 |
| Cortisol | 10.54 | 6.25 | 7.66 | 5.79 | 4.18 | 7.57 | 5.59 | 6.04 |
| (mmol/l) | (7.54) | (3.48) | (3.83) | (2.87) | (1.56) | (4.04) | (3.65) | (5.65) |
| Log | 0.92 | 0.73 | 0.83 | 0.72 | 0.59 | 0.82 | 0.67 | 0.66 |
| Transform | (0.30) | (0.24) | (0.23) | (0.21) | (0.17) | (0.22) | (0.26) | (0.30) |

Using the log transformed cortisol values as the dependent variable, a 2 (condition: stress vs control) x 3 (samples) ANOVA indicated no significant effect of condition, *F*(1, 37) = .04, *p* = .85. Sphericity was violated for the effect of sample and Greenhouse-Geisser corrections for degrees of freedom are used. There was a significant effect of sample, *F*(1.73, 64.10) = 22.16, $p < .001$, $\eta_p^2 = .38$, characterized by decreasing values from the first (prestress) sample to third (final) sample. Finally, the interaction was an significant, $F(2, 74) =$ 4.81, $p = .01$, $\eta_p^2 = .12$. To understand this effect, a 2 (condition) by 2 (Sample: 2nd sample vs $3rd$ Sample) ANOVA was computed. This indicated no main effect of condition, $F(1, 37) =$.04, $p = .85$, but a main effect of sample, $F(1, 37) = 7.72$, $p = .01$, such that the second

sample (just after stressor/control) indicated a larger cortisol output than the third sample. Further the interaction was significant $F(1, 37) = 14.57$, $p < .001$, $\eta_p^2 = .28$. Simple effects analyses of sample across conditions indicated a significant difference between the samples in the stressor condition, $F(1, 37) = 36.60$, $p < .001$, $\eta_p^2 = .50$, but not the control condition, $F(1, 37) = 0.06$, $p = 0.80$. Therefore there was no evidence this task increased cortisol in the stressor condition relative to the control condition.

Subjective Task Ratings. As in Experiments 2 and 3, after the navigation task, participants gave responses to four questions on a 0 to 100 point scale (aversion, effort, fatigue, and boredom) pertaining to the navigation task itself and a stress rating relating to the stressor tasks. These questions regarded their level of aversion, effort, fatigue, and boredom during the task. Descriptive statistics across sessions can be found in Table 22. It should be noted that the range for all variable in each session was large (all $Range \geq 70$). Participants found the navigation task more aversive during the stressor condition. Finally, participants were more subjectively more stressed by the stressor task than the control.

| | Control ($n = 36$) | Stress ($n = 36$) | t(35) | \boldsymbol{p} |
|---------------|----------------------|---------------------|-------|-------------------|
| Aversion | 19.78 (20.26) | 28.89 (25.44) | 2.85 | 0.007 |
| Effort | 21.72 (16.93) | 25.42 (18.95) | 1.36 | 0.18 |
| Fatigue | 23.81 (18.50) | 28.61 (20.86) | 1.67 | 0.11 |
| Boredom | 23.56 (20.63) | 27.50 (23.41) | 1.43 | 0.16 |
| Stress | 23.59 (25.53) | 54.06 (25.98) | 6.61 | ${}_{\leq 0.001}$ |

Table 22. Average subjective ratings after completing the Dual Solution Paradigm. Standard deviations are presented in parentheses.

Note. Some participants did not make ratings due to computer error. Paired samples t tests are presented.

Performance and Strategy in the DSP Navigation Trials. Successful navigation to the goal location occurred on 89.5% of all trials (across both conditions) within the 40-second time limit (*Mean time* = 22.19, *SD* = 9.54). A strict coding of the main strategies (shortcut, learned route, reversal of learned route, wandering, failure) accounted for 52.3% of all trials, while the rest were processed through the above coding scheme in which steps were counted to determine strategy (33.4% liberal). The rest were (14.4%) were uncodable. Numbers of trials coded as each strategy are shown in Table 23.

Table 23. Average number of trials out of 20 coded as each route selection coding by condition across order in which the two conditions were completed. Standard deviations are presented in parentheses.

| | Control First $(n = 19)$ | | Stress First $(n = 19)$ | | |
|-----------|--------------------------|---------------|-------------------------|-------------|--|
| | Control | Stress | Stress | Control | |
| Shortcut | 6.74(3.66) | 8.42(4.80) | 7.05(4.12) | 8.68 (4.52) | |
| Learned | 5.63(3.70) | 4.58(4.21) | 5.32(3.92) | 4.53(4.89) | |
| Reversal | 2.16(1.89) | 1.37(1.30) | 2.32(1.70) | 1.74(1.45) | |
| Wandering | 0.74(0.99) | 0.32(0.58) | 0.21(0.54) | 0.37(0.60) | |
| Uncodable | 3.00(1.86) | 2.58(1.90) | 3.16(1.54) | 2.74(2.00) | |

In terms of individual differences, across both sessions and conditions, participants showed a wide range of strategy preference from nearly all non-shortcut routes to all shortcuts (Control First order: Session 1 Range of $SI = .06$ to .65; Session 2 Range of $SI =$.00 to 1.00) as in the experiments above and previous research on this task. The same was true for the second order (Stress First order: Session 1 Range of SI = .00 to .75, Session 2 Range of $SI = .00$ to $.85$). As can be seen in Figure 15, there was a strong positive correlation between the two conditions, $r(36) = .64$, $p < .001$, indicating participants typically used the

same strategy between sessions, regardless of session type.

Figure 15. Scatterplot of the Solution Index measure from both control and stress sessions indicating high similarity of strategy behavior across sessions and order.

Effect of Stress on Performance in the DSP Navigation Trials. As can be seen in Table 24, there were only small differences in success rates across conditions. Using a 2 (stressor condition) x 2 (order) ANOVA on the number of successful navigation trials, there was no main effect of condition, $F(1,36) = 2.28$, $p = .14$. There was no main effect of order, $F(1,36) = .27, p = .61$. Finally, there was no interaction between condition and order, $F(1,$ 36) = 2.28, $p = 0.14$.

It is possible that stress only influenced the outset of each set of navigation trials. Therefore, an analysis was conducted across each set of ten trials. Using a 2 (stressor condition) x 2 (set: first ten trials vs second ten trials) x 2 (order) ANOVA was conducted on the number of shortcut trials. There were no main effects nor interactions, all $F(1, 36) \le 2.61$ all $p \ge 0.12$. These analyses indicate that participants were navigating as effectively in the

scheduling task (stress) session as in the word search (control) session.

Effect of Stress on Strategy in the DSP Navigation Trials. Using a 2 (stressor condition) x 2 (order) ANOVA using solution index as the dependent variable, there was no main effect of condition on solution index, $F(1, 36) = .07$, $p = .79$. No main effect of order was found, $F(1, 36) = 0.04$, $p = 0.85$. Finally, there was a significant interaction between condition and order, $F(1, 36) = 16.29$, $p < .001$, $\eta_p^2 = .31$, indicating a general practice effect across sessions. Descriptive statistics for solution index can be found in Table 24. Further, Figure 16 shows change in strategy between sessions across order type. The gray circle represents solution index during the control session while the dark gray triangle represents strategy during the stressor session. Their descending order of participants is based on performance in the first task completed. The line connecting them represents the amount of change across session. As with Experiments 2 and 3, the takeaway from this plot is the practice effect.

Figure 16. Dumbbell plots showing solution index values for each condition across order. Light gray circles represent solution index during the control session (word search) and dark gray triangles represent solution index during the stress (scheduling task).

In these navigation trials, participants sometimes change routes within a trial and walk on steps they have already traversed, or retrace their route. It is possible that stress leads to more retracing through directional confusions. A 2 (condition) by 2 (order) ANOVA on the number of retrace trials indicated no significant main effects nor an interaction, all *F*(1, 36) \leq 1.76, all $p \geq .19$.

Finally, it is possible that stress had greater effects on shortcutting behavior during the first half of trials rather than the last half. A 2 (stressor condition) x 2 (set: first vs second

half of trials) x 2 (order) ANOVA using number of shortcuts as the dependent variable indicated no main effects of conditions, $F(1, 36) = .003$, $p = .95$, nor order, $F(1, 36) = .05$, *p* = .83. However, there was a main effect of set, $F(1, 36) = 10.01$, $p = .003$, $\eta_p^2 = .22$, such that more shortcuts were taken in the second half $(M = 4.24, SD = 2.60)$ than the first half $(M$ $= 3.49, SD = 2.18$). There was a significant interaction between condition and order, $F(1, 36)$ $= 13.31, p = .01, \eta_p^2 = .27$, indicating a practice effect such that participants took more shortcuts on the second session of trials compared to the first. If the ANOVA were set up with session as a factor rather than condition, there would be main effect of session rather than this interaction. However, no other interactions were found, all $F(1, 36) \le 0.23$, all $p \ge 0$.63.

| | Control First $(n = 19)$ | | Stress First $(n = 19)$ | | |
|-----------------|--------------------------|---------------|-------------------------|--------------|--|
| | Control | Stress | Stress | Control | |
| Success | 18.26(1.76) | 17.26(2.35) | 18.05(2.04) | 18.05(1.75) | |
| Solution Index | 0.36(0.18) | 0.48(0.25) | 0.38(0.21) | 0.48(0.25) | |
| Time | 22.42 (3.85) | 22.46 (4.49) | 22.21 (4.22) | 21.68 (3.90) | |
| Path Efficiency | 2.47(0.38) | 2.32(0.46) | 2.36(0.38) | 2.23(0.49) | |

Table 24. Descriptive statistics of each objective measure across order in which the two conditions were completed. Standard deviations are presented in parentheses.

Note. Success was out of 20.

Effect of Stress on Efficiency in the DSP Navigation Trials. Descriptive statistics on each efficiency measure can be found in Table 24. A 2 (stressor condition) x 2 (order) ANOVA using *time* efficiency as the dependent variable, indicated no a main effect of condition, $F(1, 36) = .71$, $p = .41$, nor order, $F(1, 36) = .15$, $p = .71$. There was no interaction, all $F(1, 36) = .58$, p = .47. Finally, a 2 (stressor condition) x 2 (order) ANOVA

using path efficiency data as the dependent variable indicated no main effects of condition, $F(1, 36) = 0.02$, $p = 0.90$, nor order, $F(1, 36) = 0.62$, $p = 0.44$. However, the interaction was significant, $F(1, 36) = 4.98$, $p = .03$, $\eta_p^2 = .12$, which was derived from the effect of order such than participants were more efficient in their second session regardless of condition.

Initial movement and dwell measures. One possibility is that participants take longer to start moving on each trial when under stress. Descriptive measures for each dwell variable can be found in Table 25. Average time to first movement across trials was used as the dependent variable in a 2 (stressor condition) by 2 (order) ANOVA. No differences were found between conditions, $F(1, 46) = .21$, $p = .65$, nor order, $F(1, 46) = .03$, $p = .87$. Further there was no interaction, $F(1, 46) = 0.07$, $p = 0.78$. Another possibility is that participants struggle to navigate through the environment and stop more across trials after the scheduling task. Participants average total dwell time across trials and average number stops equal to or longer than .5s across trials was used as the dependent variable in a 2 (stressor condition) x 2 (order) ANOVA. After the scheduling task, participants stopped more ($M = 1.03$ stops, $SD =$.68) than after the word search task ($M = .76$ stops, $SD = .83$), $F(1, 36) = 6.40$, $p = .02$, $\eta_p^2 =$.15, However, there was no main effect of order, $F(1, 36) = .20$, $p = .65$, nor an interactions, $F(1, 36) = 1.56$, $p = .22$. Further, there was a main effect of condition for stops at or over .5s such that after the scheduling task participants had more stops ($M = .51$ stops, $SD = .47$) than in the word search task ($M = .35$ stops, $SD = .36$), $F(1, 36) = 8.18$, $p = .007$, $\eta_p^2 = .19$. Again, however, there was no main effect of order, $F(1, 36) = .07$, $p = .79$, nor an interaction, $F(1, 16) = .07$ $36) = 1.64$, $p = 0.21$.

| | Control First $(n = 19)$ | | Stress First $(n = 19)$ | | |
|-------------------------|--------------------------|---------------|-------------------------|------------|--|
| | Control | Stress | Stress | Control | |
| Initial Movement | 1.67(0.66) | 1.68(0.73) | 1.68(0.50) | 1.62(0.46) | |
| Dwell Counts | 0.78(0.81) | 0.92(0.80) | 1.16(0.85) | 0.75(0.54) | |
| Half Second Stops | 0.40(0.45) | 0.49(0.54) | 0.52(0.41) | 0.30(0.26) | |

Table 25. Descriptive statistics of each measure of dwelling across order in which the two conditions were completed. Standard deviations are presented in parentheses.

Correlations of Performance Measures with Self-Report Measures. A higher SOD was related to more success in the control session, $r(36) = .37$, $p = .02$. However, there were no significant correlations between the SBSOD and the subjective task ratings. The more fatiguing the participant found navigation in the stress condition, the more time they took to navigate, the farther they went on average, and less efficient their navigation, all $r(36) \ge 36$, all $p \leq .03$.

Analysis of individual differences in cortisol and navigation. As noted above, there were large individual differences in cortisol expression within condition. In the following analyses, participants were grouped by their log transformed cortisol reaction via a regression of their stress condition cortisol on their control day cortisol values. Residuals from this analysis were such that positive values indicated more reaction to the stress than the control condition. A median split was performed on the residuals (*Mdn* = -0.01). Nineteen participants were categorized as high responders and 19 were categorized as low responders.

A 2 (condition) by residual median split (high vs low) repeated measures ANOVA was conducted using each measure of interest in the DSP as the dependent variable (i.e., success, consistency of strategies used, solution index, time efficiency, path efficiency, time to first movement, and stop count and stop time). This analysis would indicate whether those at the highest levels of stress were more affected by that stress in terms of navigation strategy.

There were no main effects nor interactions for navigation success (number of successful trials), all $F(1, 36) \le 2.15$, all $p \ge .15$, consistency of navigation strategy, $F(1, 36)$ ≤ 1.48, all $p \ge 0.23$, nor for time to first movement, $F(1, 36) \le 1.65$, all $p \ge 0.21$.

In terms of solution index data, it was predicted that participants more affected by the stressor would take fewer shortcuts overall. No main effects of condition nor residual split were found, $F(1, 36) \le 0.35$, all $p \ge 0.56$. However, an interaction was found, $F(1, 36) = 5.07$, *p* $= .03$, $\eta_p^2 = .12$, such that the low responders took fewer shortcuts in the stress condition (*M* = .42, $SD = .26$) compared to the control condition ($M = .48$, $SD = .24$) and the high responders took more shortcuts in the stress condition $(M = .44, SD = .21)$ relative to the control condition ($M = 0.37$, $SD = 0.19$). This finding is contrary to the prediction.

It was predicted that those more affected by the stressor would be less efficient in navigation. In terms of time efficiency, no main effects were found, $F(1, 36) \leq .82$, all $p \geq$.37, but there was a significant interaction, $F(1, 36) = 6.25$, all $p = .02$. Simple effects indicated that the low responder group took longer, $F(1, 36) = 5.80$, $p = .02$, $\eta_p^2 = .15$, during the stress ($M = 22.46s$, $SD = 4.59$) compared to the control condition ($M = 21.40s$, $SD =$ 3.89), whereas the high responders showed no change, $F(1, 36) = 1.27$, $p = .27$, from the stress ($M = 22.20$ s, $SD = 4.11$) to the control condition ($M = 22.70$ s, $SD = 3.78$). A similar pattern was found in terms of path efficiency data. There were no main effects of condition or residual split, all $F(1, 36) = 0.20$, all $p = 0.67$. However, a significant interaction, $F(1, 36) =$ 4.88, $p = .03$, $\eta_p^2 = .12$, indicated that high cortisol responding participants gained in efficiency from the control ($M = 2.44$, $SD = .37$) to the stress condition ($M = 2.30$, $SD = .34$)

but low responders lost from the control ($M = 2.25$, $SD = .51$) to the stress condition ($M =$ 2.38, $SD = .50$).

Finally, navigators more influenced by the stressors were predicted to have more stops on average per trial in the DSP. As in the analysis above, there was a main effect of condition for both the stop count and half-second stop count measures. However, there was no main effect of residual split nor an interaction for either the number of stops, all $F(1, 36) \leq$.1.34, all *p* ≥ .26*,* nor half second stops, all *F*(1, 36) ≤ 1.64, all *p* ≥ .21.

This analysis indicates that there is the possibility acute cognitive stress was in some ways facilitating navigation strategies and efficiency within the DSP. Participants that were more affected by this stressor were more time efficient and path efficient. Further, the high responding participants took more shortcuts than lower responding participants.

Discussion

The cognitive fatigue task used in this experiment was not successful in elevating cortisol levels in the stress over control condition. However, as in the other two stressor tasks, there were subjective rating differences between conditions when participants considered how stressful that task was overall. This may be expected given previous literature indicating that the lack of personal control and social evaluation may be necessary for increasing cortisol in the lab (Dickerson & Kemeny, 2004; Table 1), which are not characteristic of the scheduling task.

The results found here indicate that navigation strategy and efficiency were largely unchanged between the conditions. Participants were not more inclined to navigate via learned routes in either condition. Post-hoc comparisons of each DSP measure on high and low cortisol reactors did not indicate differences in navigation performance, but did indicate significant main effects or interactions for strategy and efficiency. These results suggest a possible facilitation of navigation strategy and efficiency in the high responders compared to low-responders, such that high stress responding participants were navigating more efficiently via more shortcuts. As in Experiments 2 and 3, there was a sizeable practice effect (Boone et al., 2019) such that participants are more likely to take shortcuts in the second session, regardless of stress condition.

Table 26. Correlation table for each measure of the Dual Solution Paradigm across the stress (first row) and control (first column) **Table 26**. Correlation table for each measure of the Dual Solution Paradigm across the stress (first row) and control (first column) conditions in Experiment 4. conditions in Experiment 4.

V. Chapter 5: Comparison of Navigation across Stressor Experiments

In this dissertation, the main question concerned how stress influences human navigation strategy. However, the secondary question focused on the nature of the stressors themselves and the influence that different types of stressors might have over the navigation process. While each stress experiment itself did not show main effects of condition, there is an indication of differences between them. In this chapter, I will provide an analysis of navigation behavior across stressor experiments followed by an analysis of each stressor compared to the data from Experiment 1b.

Analysis of the stressor type on navigation strategy and efficiency. An analysis of performance across the experiments of this dissertation was undertaken. Gender was also included in this analysis to assess the overall gender effects on navigation across experiments. A 3 (experiment: CPT, Trier, Cognitive Fatigue) x 2 (condition: control vs stress) x 2 (order: Control-Stress vs Stress-Control) x 2 (gender) repeated measures ANOVA was conducted on the solution index. There is a main effect of gender, $F(1, 113) = 28.14$, $p <$.001, $\eta_p^2 = 0.20$, such that men ($M = 0.50$, $SD = 0.20$) took more shortcuts than women ($M = 0.33$, $SD = .20$, replicating Boone et al. (2018). There was also a condition by order interaction, $F(1, 113) = 33.32$, $p < .001$, $\eta_p^2 = .23$, largely reflecting an effect of practice on the task over the two sessions, regardless of condition. No other main effects or interactions were significant.

There was a main effect of gender such that men completed trials faster on average $(M = 19.90s, SD = 3.79)$ than women $(M = 24.20s, SD = 3.50)$, $F(1, 113) = 48.46$, $p < .001$, $\eta_p^2 = 0.30$. There was a main effect of gender on path efficiency such than men (*M* = 2.18, *SD*)

 $=$.43) were more path efficient than women ($M = 2.51$, $SD = .42$), $F(1, 113) = 23.43$, $p <$.001, η_p^2 = .17. Path efficiency also indicated a condition x order interaction, *F*(1, 113) = 4.24, $p = .04$, $\eta_p^2 = .04$, again reflecting a practice effect.

There were no main effects nor interactions for retracing the route, $F(1, 113) \le 2.94$, $p \ge 0.06$. In terms of initial movement times, there was a main effect of gender, $F(1, 113) =$ 20.53, $p < .001$, $\eta_p^2 = .15$, such that men ($M = 1.49$ s, $SD = .46$) initiated movement in the maze trials on average earlier on the trial than women $(M = 1.97, SD = .72)$. There was also an interaction between experiment, condition, and gender, $F(1, 113) = 3.55$, $p = .03$, $\eta_p^2 =$.06, arising from a reduction in initial movement time in cognitive fatigue task for women.

Finally, in terms of the count of stops lasting at least .5s or more (half second stops), there was a main effect of condition, $F(1, 113) = 6.66$, $p = .01$, $\eta_p^2 = .06$, such that participant took more half second stops in the stress condition ($M = .41$, $SD = .45$) than the control ($M =$.34, $SD = .35$) across all experiments. There was also a main effect of gender, $F(1, 113) =$ 29.21, $p < .001$, $\eta_p^2 = .21$, such that women ($M = .55$, $SD = .45$) took more half second stops than men ($M = 0.22$, $SD = 0.24$). There were no other main effects nor interactions.

Variability analysis. To examine variability across conditions for each experiment, solution index and path efficiency data were graphed as violin plots. These plots can be interpreted as the distribution of the data mirrored over the y-axis for the conditions of each experiment laid on top of each other. The red violins represent the data from the stress conditions while the black violins represent the data from the control conditions.

Figure 17. Violin plots comparing the profiles across each experiment for the solution index variable. Red violins are stress sessions, black violins are control session. The horizontal line indicates the mean of each group.

Figure 18. Violin plots comparing the profiles across each experiment for the path efficiency variable. Red violins are stress sessions, black violins are control session. The horizontal line indicates the mean of each group.

Notice, in Figures 17 and 18 (above), the wide shape of the control condition plots (black violins) compared to the narrower bump in density around the mean of the stress conditions (red violins). These profiles suggest that perhaps participants were more variable in their route selection process in the control condition, especially in the CPT and cognitive fatigue experiments. One possible interpretation of this result is that participant choose a strategy and largely stick to it within the stress conditions but, in contrast, in the control conditions when the stakes are lower participants meander and make other choices. Kolomogrov-Smirnov tests indicated a divergence from normality in CPT stress condition, likely due to the upward (or rightward skew—on a normal distribution plot), $p = .03$. All other distributions did not reach significance, all $p \ge 0.09$. Wilcoxon signed rank tests indicated no difference between the distributions of any of the stressors in the path efficiency nor solution index compared to their respective control conditions, all $Z \ge -0.78$, all $p \ge .44$.

Therefore, a second analysis was undertaken. Here, in each experiment, a variability measure was established on switching between strategies from trial to trial. For each consecutive pair of trials, participants were assigned a score of $+1$ if they held the same strategy and -1 if they changed strategy on that trial. Therefore, if a participant changed strategies on every trial, they would receive a variability score of -19. However, if a participant took the same strategy on each trial, they would receive $a + 19$.

No sample shows differences between stress and control conditions on the measure of strategy switching in a paired samples t-test, all $t \ge 0.99$, all $p \le 0.33$. However, it is interesting to note that participants were generally very inconsistent in their strategies overall. This indicates that participants much more likely to switch strategies rather than to use the same strategies trial to trial. See Table 27 for a descriptive statistics on consistency of navigation

strategy. While we know from previous work that most participants split their strategy behavior across trials, this effect has not been shown in previous literature on the Dual Solution Paradigm task at the level of trial to trial. Further, a 3 (Experiment) x 2 (condition) repeated measures ANOVA indicated no main effects, both $F(1, 122) \le 1.64$, both $p \ge .20$, nor an interaction, $F(1, 122) = .07$, $p = .93$.

Table 27. Average trial to trial strategy switching variability in each stress experiment in this dissertation indicating high degree of variability in navigation strategy switching. Standard deviations are presented in parentheses.

| | Stress Experiment | | | |
|---------------|--------------------------|---------------|-------------------|--|
| | Cold Pressor | Trier | Cognitive Fatigue | |
| Control | $-5.08(7.71)$ | $-6.85(8.14)$ | $-6.00(5.99)$ | |
| Stress | $-4.63(7.32)$ | $-6.03(7.18)$ | $-5.05(6.25)$ | |

Comparison of each experiment to baseline control data. This section will provide a comparison of each condition within each stressor experiments with the data from Experiment 1b, which served as the baseline data for the navigation experiment itself. Two general comparisons will be carried out on each stressor experiment, first using the data from the stress sessions, then using the data from the control.

Experiment 2 - Cold Pressor Task. Compared the data from Experiment 1b, participants in the Cold pressor stress condition were more successful, found more shortcuts, and more efficient than those in Experiment 1b, all $t(86) \ge 2.47$, all $p \le .02$. Similarly, in control condition in Experiment 3, participants were more successful, found more shortcuts, and were more efficient that those in Experiment 1b, all $t(86) \ge 2.13$, all $p \le .04$.

Experiment 3 – Trier Social Stressor Task. Participants in the Trier Social Stress condition (public speaking) did not differ from the control Experiment 1b data in terms of success on navigation, $t(77) = 1.12$, $p = .26$, or shortcutting, $t(77) = 1.46$, $p = .15$. However, the social stress participants were significantly more efficient, $t(77) = 2.17$, $p = .03$. In the control condition, participants did not differ from Experiment 1b, all $t(77) \le 1.61$, all $p \ge .11$.

Experiment 4 – Cognitive Fatigue Task. Participants in the mentally fatiguing scheduling condition were not more successful than those in Experiment 1b, $t(76) = .57$, $p =$.57. However, these participants took more shortcuts than the participants in Experiment 1b, $t(76) = 2.72$, $p = .01$, and were more efficient, $t(76) = 2.00$, $p = .05$. Similarly, when in the control condition, there was no difference in success, $t(76) = 1.63$, $p = .11$. However, more shortcuts were taken in the word search control condition in this task than in the Experiment 1b, $t(76) = 2.72$, $p = .01$.

In summary, this analysis indicates that the physical and mental stressors were not necessarily negatively affecting hippocampus-based navigation strategies, and even potentially leading to better activation of those strategies. However, in the case of the Trier Social Stressor Task, in both the stress and control conditions, participants were navigating less effectively than their counterparts in the other stressors but similarly to those in Experiment 1b.

VI. Chapter 6: General Discussion

The hypothesis that stress influences learning and memory has been considered in last decade. It has been known for many years that the hippocampus houses "place cells" that code places within the environment regardless of view (O'Keefe and Nadel, 1978) and other important spatial neurons. Further, the hippocampus has the most glucocorticoid receptors in the brain (McEwen et al., 1968). Arising from these findings was the hypothesis that cortisol elicited through stress may functionally block hippocampus-based navigation strategies and render flexible "cognitive map" like navigation (via shortcutting) inaccessible, while sparing route-taking navigation. Several literature streams have converged to show that deactivation of various brain areas through stress (Pruessner et al., 2008; Oei et al., 2007) leads a situation very similar to that predicted by this hypothesis (Packard and McGaugh, 1996; de Quervain et al., 1998). Further, memory for words can be hindered (or enhanced) in humans by stress (Andreano and Cahill, 2006, de Quervain et al., 2000) and people use previously used routes when navigating under increasing time pressure (Brunyé et al., 2016). However, other work has shown minimal or no effects of stress on navigating under other forms of stress (see Table 1; Thomas et al. 2010, Ruginski et al., 2018). On the side of learning and spatial memory under stress, results indicate a preference for complex, allocentric modes of navigation (Duncko et al., 2007; van Gervan et al., 2016). However, no studies have specifically looked at the influence of stress on navigation strategy, that is, how someone chooses to carry out a navigation task.

Results from this growing body of research indicates that the effect of stress on spatial memory is specific in two ways. First, the placement of the stressor relative to learning is vital such that stress has more of an effect after learning (de Quervain et al., 1998;

2000). Further, the type of stressor is important such that physiological stressors show lower rates of cortisol than do psychosocial stressors (Kemeny & Dickerson, 2004). In this dissertation, several experiments were conducted to examine the influence of a variety of stressors applied after learning a maze layout on navigation strategy. Each of the three main experiments tapped distinct real-world type of stressors (either physiological, social, or cognitive) in order to evaluate their effects on navigation strategy and efficiency. The general procedure was for participants to learn a maze layout in first person perspective on a desktop computer. After learning, they were exposed to the stressor or an active control in counterbalanced order across days. After the stressor, they rated their level of stress and gave a saliva sample to measure cortisol levels. At about one hour after learning the maze layout, and about 30 minutes after the stressor, participants returned to the desktop environment and were asked to navigate between learned locations. On each trial, participants could navigate in any manner they chose, but could navigate via the learned path or a shorter shortcut path. Their strategy on this task was measured by how many shortcuts were taken out of the number of trials in which they successfully found the goal (by any path). Other measures were collected included average time to the goal, path efficiency, time to first movement, number of stops, and stops over one half second. Further, participants gave ratings on how averse, fatigued, strenuous, and boring they felt the navigation task was for them.

The main results are as follows. First, participants reported finding all stressor conditions as more stressful than their respective active control conditions. This was especially true in the case of the cold pressor task (CPT) experiment (Experiment 2). Second, although the CPT and the Trier social stressor task (Experiment 3) were found to elevate cortisol above baseline relative to their control conditions, this was not true of the cognitive

fatigue task relative to control in Experiment 4. However, there were substantial individual differences in level of cortisol response due to the stressor in each experiment.

In each experiment, measures of navigation performance, including success in reaching the goal, solution index, and efficiency were compared between the stressor condition and the control using the order of the conditions as a between subjects' factor. In no experiment was a significant difference found between stress and control conditions on the navigation measures. Specifically, stress did not cause participants to globally change their navigation strategy in order to find goals within the environment. In fact, there were strong correlations between navigation strategy across the stress and control conditions, suggesting that people were generally consistent in the strategy they used across conditions. In general, what was found was a substantial practice effect such that participants took more shortcuts in their second testing session regardless of condition. Very few participants shifted towards fewer shortcuts or worse efficiency overall.

Intercorrelations within a condition across conditions indicated significant findings. The subjective ratings of the task were highly correlated such that if one found the navigation task aversive or fatiguing on the control condition, they also found it aversive or fatiguing on the stress session. However, the correlations between the objective measures and subjective measures were less robust and although some correlations were significant they were generally small. Finally, sense of direction did not generally predict strategy in any experiment or condition except in terms of success in the control cognitive fatigue and stress in the Trier experiment.

Given the large individual differences in reaction to the stressors, post-hoc analyses were conducted comparing participants whose cortisol value increased with stress versus

those who did not show an increase with stress. Overall, in Experiments 2 and 3, these analyses indicated little influence of the size of the cortisol reaction (to stress) over navigation performance, strategy, efficiency, or initial movement or dwell times. In Experiment 4, however, the results suggested a potential facilitation of navigation strategy and efficiency, such that participant were taking more shortcuts and were more efficient under stress.

Cross experiment analyses. Next, each stressor experiment was compared to the others to determine the effects across stressors. No main effect of experiment was found for any variable of interest. However, interestingly, when comparing the data from each stressor experiment to the baseline control data (Experiment 1b) differences were found between two of stressor experiments (both stress *and* control). Participants in the CPT and the cognitive fatigue experiments were generally more likely to take shortcuts and thus were more efficient in the stress condition than participants in Experiment 1b (who did not experience stress). However, there was no difference in these measures between participants who experienced the Trier that those in Experiment 1b.

Taken together, these findings indicate that navigation strategy and efficiency are robust to acute stress in contrast to the way predicted by the hippocampal-stress deactivation hypothesis derived from the literature. In what follows, I explore some potential explanations for these findings and the future of this work. The first possible explanation is that these participants were not sufficiently under stress in order to claim they were navigating with stress and effectively without stress in the control condition. A second possibility is that the stressors were not contextually specific to the navigation and an exploration of contextual

effects of navigation under stress is necessary. Finally, there is an exploration of whether stress/cortisol influences navigation at all.

Stressors. The first possible explanation of the general result that stress does not globally influence navigation strategy is that participants in this set of studies were not sufficiently stressed to observe the predicted effects. In comparison to the previous studies using the cold pressor task and the trier stressor, the results reported here are mixed. In terms of the cold pressor task using bilateral foot submersion, similar levels of circulating cortisol were found after the stressor was applied (Larra et al., 2015). For the Trier Social Stress task, as seen in Table 1, the values range more widely in the literature (Dickerson & Kemeny, 2004). The results of Experiment 3 indicated a slightly lower amount of cortisol relative to previous literature. Despite evidence in the literature that the active control of the Trier task would not cause sufficient stress to elicit cortisol (Dickerson et al., 2008; Het et al., 2009), there was a relatively large peak in cortisol in the control condition. This indicates that a tighter control condition is necessary for future testing. Finally, the cognitive fatigue scheduling task has not been evaluated in terms of cortisol output. Here, it was found that both conditions (stress and control) elicited a moderate amount of cortisol indicating that this task is not sufficient to elicit large cortisol release. Finally, it should be noted that none of these values rise to the level found in the studies in which pills were administered to elicit the stress response.

Were the participants under stress while navigating? The effect of stress on the body has various time courses depending on which predictor is in question. Heart rate and blood pressure are influenced quickly by an aversive stimulus while cortisol has a time-lagged effect. Further, there are individual differences in both the amount of cortisol released per the

stressor. It seems apparent that some people do not find public speaking too stressful, while others are highly stressed by even the idea of public speaking. One of the major methodological concerns for the work presented here is whether the participants could be considered "stressed" throughout the course of the experiments. Clearly, the processes of entering the lab and being prepped with physiological and EEG recordings for Experiments 2, 3, and 4 were stressful as indicated by large pre-task (baseline) concentrations of cortisol. Participants then engaged in two learning tasks (picture stimuli for recognition memory and maze learning for the navigation task). Then, participants were introduced to their respective stressor or active control condition. In the case of Experiment 2 (CPT) and Experiment 4 (cognitive fatigue), cortisol would most likely be on the decline. However, in Experiment 3 (Trier), the average pre-stressor cortisol was lower and thus more likely closer to a true baseline value. Then, after the stressor, participants were tested on two tasks (response inhibition and visual search) followed by the navigation task. At this point, it is likely that cortisol would be falling over a period of time. The navigation task was closer to the final cortisol sample collection than the second. Only in CPT, were participants re-introduced to the cold water several times. In Experiment 3 (Trier), participants were almost equally stressed by each condition. Therefore, what this time course suggests is that it possible in Experiments 2 and 4, that participants were potentially as stressed or more aroused via cortisol at learning than at test. In Experiment 3, participants were at the lowest stress levels after learning and at a higher cortisol levels during test.

The finding of differences between the stressor experiments and the lab control study (Experiment 1b) suggests some possible effects of stress, but in the opposite direction to what the main hypothesis predicted. In that case, participants in Experiment 1b (in which no

stressor was presented) showed lower levels of performance and less shortcutting in general. One possibility is that participants entered Experiment 1b at their highest cortisol levels and thus had the disadvantage of stress during the learning and testing (as suggested by the first sample of saliva in Experiments 2-4). In Experiments 2 and 4, participants only learned under high concentrations of cortisol but potentially tested under lower concentrations. However, the methodology of Experiment 1b was such that participants could be tested any time between 9am and 5pm and were not restricted on eating, drinking, smoking, or screened for physical fitness or depressive medications. This would effectively be randomizing who had high levels of stress and who did not. Second, it is possible that the overall process of navigating within the stressor experiments may have gave participants a boost, in both conditions, due to more general arousal. That is, participants in the stressor studies were at the top of the inverted U-shaped curve whereas those in Experiment 1b were all over the curve. Participants in Experiment 1b were derived from a general psychology undergraduate population that was required for course credit. Participants in Experiments 2-4 were derived from the overall UCSB student population and via word of mouth and flyers. Therefore, it is also possible that participants in Experiments 2 and 4 could have just been better navigators or just more conscientious to the overall tasks in general than those participants in Experiment 1b.

Decontextualized stress. In other work studying stress and memory, cortisone pills were used to induce the stress reaction and elicit a very large downstream effect on cortisol in saliva (de Quervain et al., 2000). This makes the undertaking of a study like this methodologically easier but decontextualizes the feeling of stress from the task itself. Imagine taking a cortisone pill and waiting in the lobby of lab. Then, after about 20 minutes,

the experimenter takes you to a task on learning a maze. Your body is now reacting to the cortisol in your system without a reason derived from the environment around you. Human navigation likely did not evolve to move about under situations in which the internal feeling and biological reaction is completely unrelated to the given task. Therefore, another question hinges on whether and if the process of navigating under stress in Experiments 2-4 was wholly disconnected and decontextualized from the stressor itself. Only in one experiment in the literature is the predicted effect of stress found on navigating from prior knowledge, although they did not measure cortisol (Brunyé et al., 2016). Further, it is unclear where the amount of cortisol elicited from a 25mg corticosterone pill is similar to what would be expected from the rodent studies using foot shocks. Finally, it is so relevant that when rodents are stressed in these studies, the stressors are extremely aversive (foot shocks, restraints) and the task of swimming in the milky water of the Morris Water Maze is also not an ideal situation for the rodent. However, those sorts of stressors , swimming in water and restraint, are situations that could very well play out during the course of the rodent's life and should be avoided. This is something we have not done in the lab for both practical and ethical reasons.

Many scenarios exist in which one would be under stress and navigating from prior knowledge of the environment. For instance, driving with friends or colleagues can be placed at the lower end of this spectrum. This would bring the social stressor online to the task of navigating from prior knowledge. Real emergency egress scenarios can be placed at the upper limit. Here, one would need to evacuate a building in order to survive. Meng and Zheng (2014) investigated the relationship of stress arising from emergency egress of a building in a virtual environment and found that people in the stress condition did better than

those in the control, although they did not know the environment prior to egress. Taverniers et al. (2010; 2011b) tested the extremely high stress/arousal state of jumping from a plane, although this was not memory for space necessarily. In these much more elevated scenarios, would that be sufficient to block our spatial memories as might happen for a rat in the water maze?

Does stress influence navigation or just other cognitive processes? From many studies in the literature, we know that word list learning and memory recall can be impaired due to stress. However, it is possible that the retrieval of spatio-temporal memories under stress could be insufficient stress to break the bond of the memory association. Spatial memories require a binding that is not necessarily present during word list tasks. When we navigate, we connect the "when" and the "where" in order to represent the environment. Therefore, a question remains as to whether spatial memories may be stronger than other types of declarative memories? Finally, it is possible that the effect of stress on navigation is happening at the lowest levels of cognition, rather than on the navigation process per se. Navigation is a long-term cognitive process playing out over several minutes rather than in a few seconds. While the participants might have been under the effects of stress, and thus other cognitive processes like eye gaze control, and attentional processes were affected, cortisol may not have influenced navigation preferences. As one navigates the maze on a given trial, many cues are present to influence the decision-making processes such as local turns and other objects that guide the process to carry out a route. This provides a much richer context in which to navigate and arrive at a goal rather than relying completely on one's internal representation of the space itself.

Navigation in the Dual Solution Paradigm. While negative effects of stress on navigation strategy and efficiency were not robust in this set of experiment, there are several points to be made relating to navigation within the Dual Solution Paradigm regardless of stress. First, the results found here are similar to what has been found previously in the literature using this task. For instance, there is a wide range of navigation strategies used in all three stressors, for each condition (Marchette et al., 2011; Furman et al., 2014; Weisberg & Newcombe, 2016; Boone et al., 2018). Further, in two stressor studies, there were large practice effects found in terms of the solution index (Experiments 3 and 4) and efficiency measures (Experiment 4). This was not found in Experiment 1b in which there was a nonsignificant effect of practice. Finally, as noted in Chapter 5, there were substantial sex differences in the objective measures of interests as have been documented previously (Boone et al., 2018).

Next, there were significant correlations between the SBSOD and subjective ratings within the control session indicated that participants with lower SOD scores found the task more strenuous and fatiguing. Similarly, in Experiment 3, more fatigue and boredom were significantly correlated with lower SOD scores. These correlations, however, were not found in Experiment 4.

Further, consistency in navigation was compared across conditions and experiments. This analysis indicated that participants were generally highly inconsistent in their route choice behavior from trial to trial. Although prior literature has indicated that people are more likely to execute either shortcuts or learned routes (middle of the Solution index distribution), it has not been documented at the trial to trial level of granularity. Notably, participants were more likely to switch strategies than keep the strategy, trial to trial. In

general, if a navigator were highly place-like (that is likely to take a shortcut) then you might expect them to be consistent in their navigation route choices, but this was not often seen across navigators. This could arise from low levels of learning used in this task. In previous work using this task, learning was conducted in nine passive trials (Marchette et al., 2011), whereas Boone et al. (2018) and the research in this dissertation used five active trials. Further, these effects are relegated completely to the virtual environment. Real world navigation may reveal more shortcutting (place-like performance). Future work will need to test more learning tour to test its effects.

Finally, in a recently conducted study which forms part of the data for Experiment 1b, Boone, Maghen, and Hegarty (2019) found that the instructions used in the DSP task greatly influence behavior in the task such that when asked to take shortcuts rather than "go to goal" participants are much more likely to take shortcuts. This indicates that, when left up to the participants, their strategy does not necessarily reflect their ability in this task. This is potentially very relevant in case in which emergency egress is necessary. For instance, a slight instructional manipulation to the current experiments could ask participants to find the goals as fast as possible rather than "navigate to the harp." In this way, ability and strategy may further separate.

It is interesting that the participants took more shortcuts in two of the stress studies than in Experiment 1b, regardless of condition. This could be due to reflection time outside of the experiment between sessions 4 and 5. For instance, when participants realize they can get out of the study faster if they just take the shorter paths, they may learn differently in session 5. This same situation would be less noticeable to participants in the case of Experiment 1b where the lag between sessions was just a few minutes. Therefore, it is

possible that people were incentivized to actually show their ability rather than strategy in the stress studies regardless of session.

Final thoughts and conclusions. In this dissertation, navigation under stress was tested with several stress manipulations. Participants did not generally navigate differently when in the stress condition or the active control conditions. In general, there were large effects of practice. Interestingly there were differences in navigation strategy between two experiments (cold pressor experiment and the cognitive fatigue) and the control data from Experiment 1b indicating that participants were navigating with more shortcuts in the stressor conditions and control conditions. This finding did not extend to the Trier social stress task experiment. Given the nature of the relatively minimal effects of these stressors on salivary cortisol and behavior, it is questionable whether stress influences our navigation strategy or if the stressors were just not sufficient to produce a shift in behavior. A task scenario akin to emergency egress more contextualized to when a given strategy is absolutely vital may be necessary in order to observe shifts in behavior due to stress. Further, a question remains as to whether, given the individual differences in strategy behaviors in general, navigation ability should be the next focus of this work. Overall, although we face acute stressors in our daily lives ranging in type and level of severity, this dissertation indicates that our navigation strategies are largely robust to that stress.

References

- al'Absi, M., Petersen, K. L., & Wittmers, L. E. (2002). Adrenocortical and hemodynamic predictors of pain perception in men and women. *Pain*, *96*(1-2), 197-204.
- Andreano, J. M., & Cahill, L. (2006). Glucocorticoid release and memory consolidation in men and women. *Psychological Science*, *17*(6), 466-470.
- Baum, A., & Grunberg, N. (1997). Measurement of stress hormones. In S. Cohen, R. C. Kessler, and L. U. Gordon (Eds.), Measuring Stress: A guide for health and social scientists (pp. 175–192). New York: Oxford Press.
- Birkett, M. A. (2011). The Trier Social Stress Test protocol for inducing psychological stress. *Journal of visualized experiments: JoVE*, (56), e3238.
- Bohbot, V. D., Lerch, J., Thorndycraft, B., Iaria, G., & Zijdenbos, A. P. (2007). Grey matter differences correlate with spontaneous strategies in a human virtual navigation task. *The Journal of Neuroscience*, *27*(38), 10078-10083.
- Boone, A. P., Gong, X., & Hegarty, M. (2018). Sex differences in navigation strategy and efficiency. *Memory & Cognition*, *46*(6), 909-922.
- Boone, A. P., Maghen, B. & Hegarty, M. (2019). Instructions Matter: Individual and Sex Differences in Navigation Strategy and Ability. *Memory & Cognition*.
- Brunyé, T. T., Wood, M. D., Houck, L. A., & Taylor, H. A. (2016). The path more traveled: time pressure increases reliance on familiar route-based strategies during navigation. *The Quarterly Journal of Experimental Psychology*, *70*(8), 1439-1452.
- Buchanan, T. W., Tranel, D., & Adolphs, R. (2006). Impaired memory retrieval correlates with individual differences in cortisol response but not autonomic response. *Learning & Memory*, *13*(3), 382-387.
- Credé, S., Thrash, T., Hölscher, C., & Fabrikant, S. I. (2019). The acquisition of survey knowledge for local and global landmark configurations under time pressure. *Spatial Cognition & Computation*, 1-30.
- de Kloet, E. R., Oitzl, M. S., & Joëls, M. (1993). Functional implications of brain corticosteroid receptor diversity. *Cellular and Molecular Neurobiology*, *13*(4), 433- 455.
- de Quervain, D, J. F., Roozendaal, B., & McGaugh, J. L. (1998). Stress and glucocorticoids impair retrieval of long-term spatial memory. *Nature*, *394*(6695), 787-790.
- de Quervain, D, J. F., Roozendaal, B., Nitsch, R. M., McGaugh, J. L., & Hock, C. (2000). Acute cortisone administration impairs retrieval of long-term declarative memory in humans. *Nature Neuroscience*, *3*(4), 313-314.
- de Quervain, D. J. F., Henke, K., Aerni, A., Treyer, V., McGaugh, J. L., Berthold, T., ... & Hock, C. (2003). Glucocorticoid-induced impairment of declarative memory retrieval is associated with reduced blood flow in the medial temporal lobe. *European Journal of Neuroscience*, *17*(6), 1296-1302.
- Defiore, C.H., Turner, B.B. (1983) [³H]Corticosterone binding in the caudate-putamen. Brain Research, *278*, 93–101
- Dickerson, S. S., & Kemeny, M. E. (2004). Acute stressors and cortisol responses: a theoretical integration and synthesis of laboratory research. *Psychological Bulletin*, *130*(3), 355-391.
- Dickerson, S. S., Mycek, P. J., & Zaldivar, F. (2008). Negative social evaluation, but not mere social presence, elicits cortisol responses to a laboratory stressor task. *Health Psychology*, *27*(1), 116-121.
- Duncko, R., Cornwell, B., Cui, L., Merikangas, K. R., & Grillon, C. (2007). Acute exposure to stress improves performance in trace eyeblink conditioning and spatial learning tasks in healthy men. *Learning & Memory*, *14*(5), 329-335.
- Furman, A. J., Clements-Stephens, A. M., Marchette, S. A., & Shelton, A. L. (2014). Persistent and stable biases in spatial learning mechanisms predict navigational style. *Cognitive, Affective, & Behavioral Neuroscience*, *14*(4), 1375-1391.
- Gagnon, S. A., & Wagner, A. D. (2016). Acute stress and episodic memory retrieval: neurobiological mechanisms and behavioral consequences. *Annals of the New York Academy of Sciences*.
- Hegarty, M., Richardson, A. E., Montello, D. R., Lovelace, K., & Subbiah, I. (2002). Development of a self-report measure of environmental spatial ability. *Intelligence*, *30*(5), 425-447.
- Hegarty, M., & Waller, D. (2004). A dissociation between mental rotation and perspectivetaking spatial abilities. *Intelligence*, *32*(2), 175-191.
- Herman, J. P., Patel, P. D., Akil, H., & Watson, S. J. (1989). Localization and regulation of glucocorticoid and mineralocorticoid receptor messenger RNAs in the hippocampal formation of the rat. *Molecular Endocrinology*, *3*(11), 1886-1894.
- Het, S., Ramlow, G., & Wolf, O. T. (2005). A meta-analytic review of the effects of acute cortisol administration on human memory. *Psychoneuroendocrinology*, *30*(8), 771- 784.
- Het, S., Rohleder, N., Schoofs, D., Kirschbaum, C., & Wolf, O. T. (2009). Neuroendocrine and psychometric evaluation of a placebo version of the 'Trier Social Stress Test'. *Psychoneuroendocrinology*, *34*(7), 1075-1086.
- Hines, E. A., & Brown, G. E. (1932). A standard stimulus for measuring vasomotor reactions: its application in the study of hypertension. *Proc Staff Meet Mayo Clin*, 332.
- Iaria, G., Petrides, M., Dagher, A., Pike, B., & Bohbot, V. D. (2003). Cognitive strategies dependent on the hippocampus and caudate nucleus in human navigation: variability and change with practice. *The Journal of Neuroscience*, *23*(13), 5945-5952.
- Ishikawa, T., & Montello, D. R. (2006). Spatial knowledge acquisition from direct experience in the environment: Individual differences in the development of metric knowledge and the integration of separately learned places. *Cognitive Psychology*, *52*(2), 93-129.
- Kemeny, M. E. (2003). The psychobiology of stress. *Current directions in psychological Science*, *12*(4), 124-129.
- Kirschbaum, C., & Hellhammer, D. H. (1989). Salivary cortisol in psychobiological research: An overview. *Neuropsychobiology*, *22*, 150-69.
- Kirschbaum, C., Wüst, S., & Hellhammer, D. (1992). Consistent sex differences in cortisol responses to psychological stress. *Psychosomatic Medicine*, *54*(6), 648-657.
- Kirschbaum, C., Pirke, K.M., Hellhammer, D.H., 1993. The 'Trier Social Stress Test'—a tool for investigating psychobiological stress responses in a laboratory setting. Neuropsychobiology, *28*, 76–81.
- Kirschbaum, C., Wolf, O.T., May, M., Wippich, W., Hellhammer, D.H., 1996. Stress- and treatment-induced elevations of cortisol levels associated with impaired declarative memory in healthy adults. *Life Sciences*, *58*, 1475–1483.
- Klopp, C., Garcia, C., Schulman, A. H., Ward, C. P., & Tartar, J. L. (2012). Acute social stress increases biochemical and self report markers of stress without altering spatial learning in humans. *Activitas Nervosa Superior Rediviva*, *33*(4), 15-20.
- Kudielka, B. M., Hellhammer, D. H., & Wüst, S. (2009). Why do we respond so differently? Reviewing determinants of human salivary cortisol responses to challenge. *Psychoneuroendocrinology*, *34*(1), 2-18.
- Kumaran, D., & Maguire, E. A. (2005). The human hippocampus: cognitive maps or relational memory? *The Journal of Neuroscience*, *25*(31), 7254-7259.
- Larra, M. F., Schilling, T. M., Röhrig, P., & Schächinger, H. (2015). Enhanced stress response by a bilateral feet compared to a unilateral hand cold pressor test. *Stress*, *18*(5), 589-596.
- Lawton, C. A. (1994). Gender differences in way-finding strategies: Relationship to spatial ability and spatial anxiety. *Sex Roles*, *30*(11-12), 765-779.
- Lawton, C. A., & Kallai, J. (2002). Gender differences in wayfinding strategies and anxiety about wayfinding: A cross-cultural comparison. *Sex Roles*, *47*(9-10), 389-401.
- Lawton, C. A., Charleston, S. I., & Zieles, A. S. (1996). Individual-and gender-related differences in indoor wayfinding. *Environment and Behavior*, *28*(2), 204-219.
- Lovallo, W. (1975). The cold pressor test and autonomic function: a review and integration. *Psychophysiology*, *12*(3), 268-282.
- Lupien, S. J., & McEwen, B. S. (1997). The acute effects of corticosteroids on cognition: integration of animal and human model studies. *Brain Research Reviews*, *24*(1), 1-27.
- Lupien, S. J., Maheu, F., Tu, M., Fiocco, A., & Schramek, T. E. (2007). The effects of stress and stress hormones on human cognition: Implications for the field of brain and cognition. *Brain and Cognition*, *65*(3), 209-237.
- Maguire, E. A., Burgess, N., Donnett, J. G., Frackowiak, R. S. J., Frith, C. D. & O'Keefe, J. (1998). Knowing where, and getting there: a human navigation network. *Science*, *280*, 921–924.
- Maguire, E. A., Woollett, K. & Spiers, H. J. (2006). London taxi drivers and bus drivers: a structural MRI and neuro- psychological analysis. *Hippocampus*, *16*, 1091–1101.
- Marchette, S. A., Bakker, A., & Shelton, A. L. (2011). Cognitive mappers to creatures of habit: differential engagement of place and response learning mechanisms predicts human navigational behavior. *The Journal of Neuroscience*, *31*(43), 15264-15268.
- McEwen, B.S., Weiss, J.M., Schwartz, L.S. (1968). Selective retention of corticosterone by limbic structures in rat brain. *Nature*, *220*, 911–912.
- Meng, F., & Zhang, W. (2014). Way-finding during a fire emergency: an experimental study in a virtual environment. *Ergonomics*, *57*(6), 816-827.
- Montello, D. R. (2005). *Navigation*. In P. Shah & A. Miyake (Eds.), *The Cambridge handbook of visuospatial thinking* (pp. 257-294). Cambridge: Cambridge University Press.
- Morris, R. G. M., Garrud, P., Rawlins, J. N. P., & O'Keefe, J. (1982). Place navigation impaired in rats with hippocampal lesions. *Nature*, *297*(5868), 681-683.
- O'Connor, P. J., & Corrigan, D. L. (1987). Influence of short-term cycling on salivary cortisol levels. *Medicine and Science in Sports and Exercise*, *19*(3), 224-228.
- O'Keefe, J., & Dostrovsky, J. (1971). The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat. *Brain Research*,*34*(1), 171-175.
- O'Keefe, J., & Nadel, L. (1978). *The hippocampus as a cognitive map*. Oxford: Clarendon Press.
- O'Keefe, J. (2007). Hippocampal neurophysiology in the behaving animal. In P. Andersen, R. Morris, D. Amaral, T. Bliss, & J. O'Keefe (Eds.). The hippocampus book (pp. 475 - 575). New York: Oxford University Press.
- Oei, N. Y., Elzinga, B. M., Wolf, O. T., de Ruiter, M. B., Damoiseaux, J. S., Kuijer, J. P., ... & Rombouts, S. A. (2007). Glucocorticoids decrease hippocampal and prefrontal activation during declarative memory retrieval in young men. *Brain Imaging and Behavior*, *1*(1-2), 31-41.
- Oitzl, M. S., & De Kloet, E. R. (1992). Selective corticosteroid antagonists modulate specific aspects of spatial orientation learning. *Behavioral Neuroscience*, *106*(1), 62.
- Ozel , F. (2001). Time pressure and stress as a factor during emergency egress. *Safety Science, 38*(2), 95-107.
- Packard, M. G., & McGaugh, J. L. (1996). Inactivation of hippocampus or caudate nucleus with lidocaine differentially affects expression of place and response learning. *Neurobiology of Learning and Memory*, *65*(1), 65-72.
- Pazzaglia, F., C. Cornoldi and R. De Beni (2000), 'Differenze individuali nella rappresentazione dello spazio e nell'abilita` di orientamento: Presentazione di un questionario autovalutativo', *Giornale Italiano Di Psicologia, 27*(3), 627–650.
- Piber, D., Schultebraucks, K., Mueller, S. C., Deuter, C. E., Wingenfeld, K., & Otte, C. (2016). Mineralocorticoid receptor stimulation effects on spatial memory in healthy

young adults: A study using the virtual morris water maze task. *Neurobiology of Learning and Memory*, *136*, 139-146.

- Pruessner, J. C., Dedovic, K., Khalili-Mahani, N., Engert, V., Pruessner, M., Buss, C., ... & Lupien, S. (2008). Deactivation of the limbic system during acute psychosocial stress: evidence from positron emission tomography and functional magnetic resonance imaging studies. *Biological Psychiatry*, *63*(2), 234-240.
- Richardson, A. E., & VanderKaay Tomasulo, M. M. (2011). Influence of acute stress on spatial tasks in humans. *Physiology & Behavior*, *103*(5), 459-466.
- Roozendaal, B. (2002). Stress and memory: opposing effects of glucocorticoids on memory consolidation and memory retrieval. *Neurobiology of Learning and Memory*, *78*(3), 578-595.
- Ruginski, I. T., Stefanucci, J. K., & Creem-Regehr, S. H. (2018, September). State Anxiety Influences Sex Differences in Spatial Learning. In *German Conference on Spatial Cognition* (pp. 244-257). Springer, Cham.
- Sandi, C., Loscertales, M., & Guaza, C. (1997). Experience-dependent facilitating effect of corticosterone on spatial memory formation in the water maze. *European Journal of Neuroscience*, *9*(4), 637-642.
- Sapolsky, R. M. (2002). Endocrinology of the stress-response. In J. B. Becker, S. M. Breedlove, D. Crews, & M. M, McCarthy (Eds.), Behavioral endocrinology (pp. 409- 449). Cambridge, MA: MIT Press.
- Schinazi, V. R., Nardi, D., Newcombe, N. S., Shipley, T. F., & Epstein, R. A. (2013). Hippocampal size predicts rapid learning of a cognitive map in humans. *Hippocampus*, *23*(6), 515-528.
- Schwabe, L., Oitzl, M. S., Philippsen, C., Richter, S., Bohringer, A., Wippich, W., & Schachinger, H. (2007). Stress modulates the use of spatial versus stimulus-response learning strategies in humans. *Learning & Memory*, *14*(1-2), 109-116.
- Schwabe, L., Haddad, L., & Schachinger, H. (2008). HPA axis activation by a socially evaluated cold-pressor test. *Psychoneuroendocrinology*, *33*(6), 890-895.
- Scoville, W. B., & Milner, B. (1957). Loss of recent memory after bilateral hippocampal lesions. *Journal of Neurology, Neurosurgery & Psychiatry*, *20*(1), 11-21.
- Selye, H. (1950). The physiology and pathology of exposure to stress. Oxford, England: Acta, Inc.
- Smeets, T., Otgaar, H., Candel, I., & Wolf, O. T. (2008). True or false? Memory is differentially affected by stress-induced cortisol elevations and sympathetic activity at consolidation and retrieval. *Psychoneuroendocrinology*, *33*(10), 1378-1386.
- Smeets, T. (2011). Acute stress impairs memory retrieval independent of time of day. *Psychoneuroendocrinology*, *36*(4), 495-501.
- Sutherland, R. J., Kolb, B., & Whishaw, I. Q. (1982). Spatial mapping: definitive disruption by hippocampal or medial frontal cortical damage in the rat. *Neuroscience Letters*, *31*(3), 271-276.
- Taatgen, N., 1999, Learning without limits: from problem solving towards a unified theory of learning. PhD Thesis, University of Groningen.
- Taverniers, J., Van Ruysseveldt, J., Smeets, T., & von Grumbkow, J. (2010). High-intensity stress elicits robust cortisol increases, and impairs working memory and visuo-spatial declarative memory in Special Forces candidates: A field experiment. *Stress*, *13*(4), 324-334.
- Taverniers, J., Smeets, T., Bue, S. L., Syroit, J., Van Ruysseveldt, J., Pattyn, N., & von Grumbkow, J. (2011). Visuo-spatial path learning, stress, and cortisol secretion following military cadets' first parachute jump: The effect of increasing task complexity. *Cognitive, Affective, & Behavioral Neuroscience*, *11*(3), 332-343
- Thomas, K. G., Laurance, H. E., Nadel, L., & Jacobs, W. J. (2010). Stress-induced impairment of spatial navigation in females. *South African Journal of Psychology*, *40*(1), 32-43.
- Unsworth, N., Heitz, R. P., Schrock, J. C., & Engle, R. W. (2005). An automated version of the operation span task. *Behavior Research Methods*, *37*(3), 498-505.
- van Gerven, D. J., Ferguson, T., & Skelton, R. W. (2016). Acute stress switches spatial navigation strategy from egocentric to allocentric in a virtual Morris water maze. *Neurobiology of Learning and Memory*, *132*, 29-39.
- Weisberg, S. M., & Newcombe, N. S. (2016). How do (some) people make a cognitive map? Routes, places, and working memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *42*(5), 768-785.
- Wiemers, U. S., Schoofs, D., & Wolf, O. T. (2013). A friendly version of the Trier Social Stress Test does not activate the HPA axis in healthy men and women. *Stress*, *16*(2), 254-260.
- Wolf, O. T. (2009). Stress and memory in humans: twelve years of progress? *Brain Research*, *1293*, 142-154.
- Yerkes, R. M., & Dodson, J. D. (1908). The relation of strength of stimulus to rapidity of habit-formation. *Journal of Comparative Neurology and Psychology*, *18*(5), 459-482.

Appendices

Appendix A – Trials Used in the Dual Solution Paradigm in Experiment 1a. The bottom four trials were omitted in Experiments 1b through 4.

Note. The purple line indicates the entire learned path. The yellow line indicates the shortcut path on this specific trial. The green and red rectangles represent the start and end location on this trial, respectively. Participants did not see this colored start or end colored squares.

Appendix B - Santa Barbara Sense of Direction Scale (Hegarty et al., 2002) SANTA BARBARA SENSE-OF-DIRECTION SCALE

Sex: F M Today's Date:

Age: $V. 2$

This questionnaire consists of several statements about your spatial and navigational abilities, preferences, and experiences. After each statement, you should circle a number to indicate your level of agreement with the statement. Circle "1" if you strongly agree that the statement applies to you, "7" if you strongly disagree, or some number in between if your agreement is intermediate. Circle "4" if you neither agree nor disagree.

1. I am very good at giving directions.

strongly agree 1 2 3 4 5 6 7 strongly disagree

2. I have a poor memory for where I left things.

strongly agree 1 2 3 4 5 6 7 strongly disagree

3. I am very good at judging distances.

strongly agree 1 2 3 4 5 6 7 strongly disagree

4. My "sense of direction" is very good.

strongly agree 1 2 3 4 5 6 7 strongly disagree

5. I tend to think of my environment in terms of cardinal directions (N, S, E, W).

strongly agree 1 2 3 4 5 6 7 strongly disagree

6. I very easily get lost in a new city.

strongly agree 1 2 3 4 5 6 7 strongly disagree

7. I enjoy reading maps.

strongly agree 1 2 3 4 5 6 7 strongly disagree

8. I have trouble understanding directions.

strongly agree 1 2 3 4 5 6 7 strongly disagree

9. I am very good at reading maps.

strongly agree 1 2 3 4 5 6 7 strongly disagree

10. I don't remember routes very well while riding as a passenger in a car.

strongly agree 1 2 3 4 5 6 7 strongly disagree

11. I don't enjoy giving directions.

strongly agree 1 2 3 4 5 6 7 strongly disagree

12. It's not important to me to know where I am.

strongly agree 1 2 3 4 5 6 7 strongly disagree

13. I usually let someone else do the navigational planning for long trips.

strongly agree 1 2 3 4 5 6 7 strongly disagree

14. I can usually remember a new route after I have traveled it only once.

strongly agree 1 2 3 4 5 6 7 strongly disagree

15. I don't have a very good "mental map" of my environment.

strongly agree 1 2 3 4 5 6 7 strongly disagree

Appendix C - Questionnaire of Spatial Representation

Questionnaire on Spatial Representation (Pazzaglia, Cornoldi & De Beni, 2000)

Instructions: This is a questionnaire on your sense of direction and how you think about different places. Please mark your answers by circling one of the numbers (1 to 5) for each question. Read each item carefully and respond to all questions.

- 1. Do you think you have a good sense of direction? 1 2 3 4 5 (not at all) (very much)
- 2. Are you considered by your family or friends to have a good sense of direction? 1 2 3 4 5

(not at all) (very much)

3. Think about the way you orient yourself as you navigate through different environments around you. Would you describe yourself as a person:

a. who orients him/herself by remembering routes connecting one place to another.

1 2 3 4 5 (not at all) (very much) b. who orients him/herself by looking for well-known landmarks. 1 2 3 4 5 (not at all) (very much) c. who tries to create a mental map of the environment 1 2 3 4 5 (not at all) (very much) 4. Think of a city that you have visited as a tourist. Write the name of the city: Now try to classify your representation of the city: a. A map-like representation

8. As you move around a complex building (store, museum) do you think spontaneously and easily about your direction in relation to the general structure of the building and the external environment?

11 When you are in a complex building (with many floors, stairs, corridors) and you have to indicate where the entrance is, how easily can you perform this task?

1 2 3 4 5 (not at all) (very well)

(not at all) (very well)

Appendix D – Dual Solution Paradigm Script

Before participant shows up, have the screen set up so it says participant number, condition, and gender if you know it.

- 1) "Hello, welcome to the experiment. Thank you for being here. My name is *_____* and I really appreciate your participation. You can leave your stuff on the ground there *{if they have anything}*. Have a seat right here. The first thing you see in front of you is an informed consent sheet that outlines your rights as a participant. Please read over this informed consent form carefully. Please ask me any questions before you sign and date it."
	- a. Answer any questions.
- 2) VR Introduction
	- a. First I need to make sure you are one meter away from the screen. I'm going to hold this string up close to your face. [As them to move back until it looks as if the string would be at approximately the back of their eyeball.]
	- b. "Just to remind you: Occasionally some people feel sick in virtual environments. If at any point during this experiment you feel sick, please let me know immediately."

i. *If they start to feel ill or get sick:* **"Please look away from the screen."** *(next to the trash can).*

- c. "Next, you will see an open environment that will help you learn how our system works. You will use the forward arrow here (*point*) to move around in the environment. To walk to the left or to the right, you will to need move the mouse in that direction. Whatever direction you are looking, you will move in that direction if you press the forward arrow. Go ahead and start walk towards the end of this hallway. When you get to the red arrow, please turn in the direction that the arrow is pointing."
	- i. *Once they have done the first arrow*: "Please continue following the arrows in the environment until I tell you to stop. [Have them go around twice.]
	- ii. "Are you comfortable with how you are going to move around?" [press g]
- 3) VR Learning Instructions
	- a. "Now you will begin the actual experiment. First you will take a tour of this new environment. Like you have done in the previous environment, please follow the arrows using the mouse and keyboard. You will go through this environment *five* times. Please pay attention to the objects in this environment as you move past them. **As you walk through this environment, please say each objects name aloud as you pass. If we are going to use a different word to refer to an object, I will tell you what that is.**
	- b. **After first loop:** "STOP. Notice that the counter changed to 4. Now you have four more to do. Do these on your own. You can stop saying the object names if you want."
		- i. Do this until the screen turns blue.
		- ii. When this ends, button ALT+G to advance to trials.
- 4) VR Trials Instructions
	- a. "For the next part of the experiment, you will be asked to move from some particular place in the environment to a target object that you saw in the environment. I'll give you a mock example of how this work. In this example your task is to travel from fan to a water fountain.
		- i. "Each trial will start when the blues screen goes away and you see you are in the environment. First you will need to orient yourself by looking around using the mouse. I will ask you 'DO YOU FEEL LIKE YOU KNOW WHERE YOU ARE?' When you say yes, I will say "Okay, please turn towards the (fan) \blacksquare ." When you are looking at the fan, I will say, "please navigate to the (water fountain) The name of the target object will also be presented on the screen. When you reach the target object, you will need to walk into the object as if you were going to knock it over with your body. When you do this, the trial will end and we will start the next trial."
		- ii. "You will have up to 40 seconds to find the target object. When you either find the target, (or the time runs out), the screen will turn blue and you will be transported to your next start location and given another object to find."
		- iii. "Do you have any questions about your objective for this task?"
		- iv. To start a trial, press G.
			- 1. When they turn towards the object and they are ready, press G and say "please navigate to the XXX" which will be presented on the screen so they can see it in the top left corner.

5) Experimental Task Routine

- a. "Are you ready for the next trial?" {*Button press to start the first trial.*}
- b. "Please orient yourself by looking around. Please let me know when you feel like you know where you are… (if they don't, ask them: Do you feel like you know where you are? If not, say: Please do one full rotation.")
- c. When they orient themselves or finish turning: "Please turn towards the (nearest object) \cdots
- d. "Please navigate to the: *XXXXXXX*"
	- i. When the trial ends, start routine again.
- e. When all trials are complete: "Okay, we are done with this part of the experiment."

i. Take a break and repeat the process for the next DSP environment.

6) Break

a. This break will last approximately 15 minutes. You may use the restroom and have a piece of candy and soda or bottle of water.

7) SECOND DSP

a. Now we are going to do the same thing we just did in a new environment. As in the previous environment, you will take a tour of this new environment. Like you have done in the previous environment, please follow the arrows

using the mouse and keyboard. You will go through this environment *five* times. Please pay attention to the objects in this environment as you move past them. **As you walk through this environment, please say each objects name aloud as you pass. If we are going to use a different word to refer to an object, I will tell you what that is.**

- b. "Just like in the last environment, for the next part of the experiment, you will be asked to move from some particular place in the environment to a target object that you saw in the environment. Would you like to hear the mock example again?
	- i. . In this mock example your task is to travel from the fan to a water fountain.
		- 1. "Each trial will start when the blues screen goes away and you see you are in the environment. First you will need to orient yourself by looking around using the mouse. I will ask you 'DO YOU FEEL LIKE YOU KNOW WHERE YOU ARE?' When you say yes, I will say "Okay, please turn towards the ____(fan)_____." When you are looking at the fan, I will say, "please navigate to the $(water \, {f}$ $)$. The name of the target object will also be presented on the screen. When you reach the target object, you will need to walk into the object as if you were going to knock it over with your body. When you do this, the trial will end and we will start the next trial"
	- ii. "As before, you will have up to 40 seconds to find the target object. When you either find the target, (or the time runs out), the screen will turn blue and you will be transported to your next start location and given another object to find."
	- iii. "Do you have any questions about your objective for this task?"

8) Second DSP Experimental Task Routine

- a. "Are you ready for the next trial?" {*Button press to start the first trial.*}
- b. "Please orient yourself by looking around. Please let me know when you feel like you know where you are… (if they don't, ask them: Do you feel like you know where you are? If not, say: Please do one full rotation.")
- c. When they orient themselves or finish turning: "Please turn towards the _____(nearest object) ____."
- d. "Please navigate to the: *XXXXXXX*"
	- i. When the trial ends, start routine again.
- 9) Qualtrics
	- a. "For the next task, you will answer a few questions on the computer."
	- b. Experimenter enters subject number and environment order.
	- c. "Now answer these questions to the best of your ability. Please read all instructions careful. Let me know if you any questions as you go.
- 10) Debriefing
	- a. That's all we have for you today. Thank you so much for participating today. We really appreciate your help. I will give credit on Sona and take your informed consent sheet off of your packet.
- b. Do you have any questions about what you did today?
	- i. This study is about understanding if navigation strategy is stable over time in VR.

FIN

Appendix E -- Phone screen questionnaire Experiments 2 through 4

In this phone call I will describe the study and I will ask you some questions. You are not obligated to answer every question. All of your answers to the questions will be confidential. After the conversation you will receive an email that will indicate whether or not you are eligible for this study. This email will come within a week. If you have any questions or concerns, you may interrupt me at any time.

The study will consist of about 13 hours spread over the course of 5 days. Participants will be compensated \$20/hour in addition to any bonuses you may get for your performance during the cognitive tasks. You will be paid an extra \$25 for completing the study.

In this study we will collect one small blood sample from you. **Are you comfortable with a small blood draw?** Additionally, we will be collecting physiological data including heart rate, blood pressure, skin conductance, and impedance cardiography. This will require us to gently exfoliate small areas of your skin and record your blood flow with non-invasive sensors. Some of the sensors will be placed around your chest area by a female RA. Additionally, we will also be placing an EEG cap on your head to record neural data. The EEG cap will leave a gel residue in your hair that can be washed off with shampoo. We ask that you arrive to these sessions with your hair freshly shampooed and dry. Finally, throughout the study, we will be taking saliva samples from you. **Are you comfortable with us taking these measurements?**

Each participant will experience one of four potential stressful stimuli. The possible stimuli are: strenuous biking on a stationary bike, briefly placing your feet in ice cold water, a cognitive fatigue, or a social stressor. Participants will be randomly selected to experience one of these stimuli. In addition to the stressful stimuli, participants will be asked to complete various forms of cognitive tasks.

Now I will describe the sessions:

Session 1 (~30-45 mins)

• In this session, you will read and sign a consent form. We will collect a small blood sample from you and screen you for motion sickness. Finally, we will have you put your feet in a bucket of ice water for 90 seconds.

Session 2 (1-1.5 hours)

• In this session, we will obtain a VO2 max measurement from you. A VO2 max is a measurement of the maximum amount of oxygen you are able to utilize during cardio exercise. In order to measure this, you will perform some breathing exercises and then bike for 10-15 minutes while physiological data is collected from you (i.e. heart rate, blood pressure, etc.). We will ask you to refrain from physical exercise 48 hours prior to this session.

Session 3 (~3 hours)

• In this session, you will complete various cognitive assessments. This session will not involve a stressful stimuli.

Sessions 4 and 5 (4-6 hours)

• In these sessions, you will complete various cognitive assessments. In one of these sessions, you will partake in a stressful stimuli.

We will also ask you to complete a 30 minute online survey that I will send to you later on. You will also be compensated for this survey.

Now I will ask you the questions, are you ready?

1.How old are you? (Age range 18-35) 2.Do you wear glasses/contacts? If they have contacts, ask to bring contacts to every session

- If they only have glasses they CANNOT PARTICIPATE (don't tell them this on the phone, they will be told via email)
- 3. What is your height and weight?
- 4. Has your doctor ever said that you have a heart condition and that you should only perform physical activity recommended by a doctor?
- 5. Do you feel pain in your chest when you perform physical activity?
- 6. In the past month, have you had chest pain when you were not performing any physical activity?
- 7. Do you lose your balance because of dizziness or do you ever lose consciousness?
- 8. Do you have a bone or joint problem that could be made worse by a change in your physical activity?
- 9. Is your doctor currently prescribing any medication for your blood pressure or for a heart condition?
- 10. Do you know of ANY other reason why you should not engage in physical activity?
- 11. Do you partake in any regular physical activity e.g. cycling, running, tennis, golf etc? If so, please explain:
- How regularly do they do cardio
- If they do not do cardio regularly, make a note
- 12. Do you have (or have you had) any pain or injuries that may be aggravated by you engaging in intense physical exercise (cycling)?
- 13. Have you had any surgeries?
- 14. Has a medical doctor ever diagnosed you with a chronic disease, such as coronary heart disease, high blood pressure, high cholesterol or diabetes?
- 15. Are you currently taking any medication (including birth control)?
- Be sure they are not taking a psychostimulant/antidepressant
- \circ Wellbutrin \rightarrow Not eligible
- \circ Adderall \rightarrow Not eligible
- 16. If you take any recreational drugs, are you willing to abstain in the 24 hours prior to each testing session?
- 17. If you workout regularly, are you willing to abstain from any strenuous workouts 48 hours prior to the VO2 Max session?
- 18. Do you wear a hairpiece/weave etc that you cannot remove?
- 19. Are you willing to have blood drawn on the first session (this will only happen one time)?
- 20. Are you willing to provide multiple saliva samples throughout each session?
- 21. Do you get motion sickness?
- 22. The physiological sensors will be placed around your chest area. Will you be ok with temporarily raising your shirt for the sensors to be placed by a female?
- 23. As part of the study you may be required to submerge your feet in a bucket of ice water for 90s. In one of the sessions you will be required to do this multiple times. Do you think this is something you will be able to cope with?
- 24. Have you ever suffered from frostbite?
- 25. As part of the study you may be required to deliver a speech and calculate math problems in front of a panel of three to four people and a video camera. Do you think this is something you will be able to cope with?
- 26. As part of the study you may bike for two hours at a relatively high resistance. Do you think this is something you will be able to cope with?

Do you have any questions for me?